PLANT RESPONSES TO GRAZER-MEDIATED HABITAT ALTERATIONS IN
TALLGRASS PRAIRIE

by

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Abstract

The effects of bison activities on forb diversity and cover have been well-established, but less is known about how forb life history is altered by bison-mediated habitat changes. This study had three main objectives: 1) to evaluate the hypothesis that release from aboveground competition with grasses may contribute to the increased cover and diversity of forbs in prairie grazed by bison relative to ungrazed prairie, 2) to determine whether differences in forb reproductive effort between grazed and ungrazed habitats were size-dependent, and 3) to look for evidence of a trade-off between allocation to vegetative and sexual reproduction.

The growth, biomass allocation, and sexual reproduction of six common unpalatable perennial species were measured and compared between bison-grazed and ungrazed tallgrass prairie burned at 2-year intervals: *Ambrosia psilostachya*, *Artemisia ludoviciana*, *Baptisia australis*, *Psoralidium tenuiflorum*, *Solidago canadensis*, and *Vernonia baldwinii*. Vegetative reproduction was also measured for *B. australis¸ S. canadensis*, and *V. baldwinii*. Light availability, canopy density and height, and percent cover of neighboring plants were measured in each studied individual's immediate neighborhood and compared between habitats to establish the possibility of differing aboveground competition.

Aboveground competition may be lower in bison-grazed habitats, as evidenced by differences in habitat characteristics and plant performance found in this study. In bison-present habitats, sexual reproduction was elevated for all six species and average plant size was greater for all species except *A. psilostachya*. Vegetative reproduction was not clearly different between habitats for all three species examined. Sexual reproduction increased with size for all species, and the relationship differed significantly between habitats for all species except *A. psilostachya*.

Allocation to vegetative reproduction was not generally related to aboveground biomass, nor was there a clear trade-off between allocation to vegetative and sexual reproduction.

The results of this study provide evidence that release from aboveground competition with grasses promotes the growth and sexual reproduction of the studied species of forb, and that differences in sexual reproduction are not entirely size-dependent. Patterns in allocation to vegetative reproduction were less clear and were not clearly tied to sexual reproductive allocation.

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Dedication

I would like to dedicate my thesis to all the plants who gave their lives for my research, albeit unwillingly. May they rest in pieces.

Chapter 1 - Forb Performance and Biomass Allocation Patterns in Grazed and Ungrazed Tallgrass Prairie

Abstract

This study compared the growth, reproduction, and biomass allocation patterns of six species of prairie forb in a single growing season between tallgrass prairie habitats with and without bison. This study was conducted to test the hypothesis that release from aboveground competition with grasses may contribute to the increased cover and diversity of forbs in prairie grazed by bison relative to ungrazed prairie. The species studied were *Ambrosia psilostachya*, *Artemisia ludoviciana*, *Solidago canadensis*, and *Vernonia baldwinii* of Asteraceae and *Baptisia australis* and *Psoralidium tenuiflorum* of Fabaceae. In order to establish the differences in resource availability between habitats with and without large grazers, several relevant attributes of the habitats immediately surrounding each studied individual were also compared, including light availability, canopy density and height, and percent cover of neighboring plants. Bison-present habitats showed greater forb diversity, bare ground, forb cover, and light availability compared to bison-absent habitats, in which grass cover, vegetation density, and canopy height were greater. In bison-present habitats, sexual reproduction was elevated for all species, average plant size was greater for five species, and vegetative reproduction was unaffected for all three species for which it was measured. Only *A. psilostachya* did not vary between treatments in size or allocation. There appeared to be a trade-off between allocation to stem and reproductive allocation, with reproductive allocation comparatively greater in bison-present habitats for five of the species studied. The results of this study provide evidence that release from aboveground competition with grasses promotes the growth and reproduction of the studied species of forb.

Over time, average increases or decreases in individual performance determine changes in plant populations. Thus, it is important to improve our understanding of how management-related environmental changes impact the growth of individuals so that we can better predict long-term changes in population dynamics in the endangered tallgrass prairie ecosystem.

Introduction

Large grazers play an important role in shaping plant community structure, diversity, and population dynamics in grassland communities (Karki et al. 2000; Koerner & Collins 2013). Large grazers such as bison can influence prairie communities in many ways: by altering nutrient cycling (Johnson & Matchett), removing biomass (Knapp & Seastedt 1986), and creating disturbances through other activities such as wallowing and trampling (Knapp et al 1999). Herbivory has been shown to affect various aspects of plant life history such as growth, survival, and reproduction (Noy-Meir 1993; Pastore & Russell 2012). These changes in life history may also affect the competitive ability of grazed plants, particularly when grazers preferentially eat certain species (Augustine & MacNaughton 1998). Even non-consumed species may be affected by alterations in habitat caused by grazer activities (Damhoureyeh & Hartnett 1997). By removing biomass, grazers may alter light availability and soil water and nutrient availability, and these changes in microclimate can be important to the soil microbiota and plant growth (Hobbs 1996; Knapp & Seastedt 1986; Knapp et al. 2012). Defecation and urination create concentrated influxes of nutrients in affected areas (Steinhauer and Collins 1995). Grazers also tend to increase the availability of bare ground, opening up space for lateral spread and for recruitment from seed or buds (England & DeVos 1969). Populations and diversity of consumers such as insects, birds, and small mammals can also be affected by grazer-mediated changes in habitat (Joern 2005; Moran 2014; Powell 2006). These alterations in habitat, particularly when coupled with shifts in competitive relationships, can have important consequences for all plant species in a community, regardless of whether they are directly subjected to herbivory or affected indirectly via alterations of the local environment (Knapp et al 1999).

Plants are non-motile organisms, so their growth and reproduction are inherently limited by the resource availability and interactions with immediate neighbors in their habitat, rather than community-wide average densities of competitors or abiotic conditions (Harper 1977). Though limited by species-specific genetic constraints, plants are able to adjust many aspects of their life history, such as growth, reproductive effort, and resource allocation patterns, in order to maximize fitness in response to environmental pressures (Hermans et al. 2006; McCarthy & Enquist 2007; Poorter et al. 2011). Plant growth is constrained by the availability of space, water, nutrients, and light, any of which resources may be limiting in tallgrass prairie.

According to Optimal Partitioning Theory, individual plants are capable of altering their growth plastically in response to environmental triggers such as resource limitation, maximizing fitness by allocating a higher percentage of resources to the growth of structures whose functions are particularly important in a given environment (Chapin et al. 1991; McCarthy & Enquist 2007). For instance, light limitation may cause an individual to increase biomass allocation to stem to compete with neighbors by increasing height (De Kroon et al. 2009). For polycarpic perennial species, individuals must balance allocation to reproduction with survival since producing a smaller quantity of propagules in any given year may lead to greater overall fitness if it enables the plant to survive longer and thus reproduce more times (Bazzaz et al 1987). Resource limitation may lead to reduced reproductive effort or fecundity in a given season, so consistent resource limitation could decrease propagation and thus lead to population decline, particularly if coupled with reduced survival rates. Clonal plant species have the additional ability to allocate resources to the creation of belowground buds or rhizomes that can increase population size and promote genet persistence without increasing population genetic diversity (Benson & Hartnett 2006; Klimesova & Klimes 2007). In environments with high temporal

and/or spatial variation in resource availability or consumer pressure like the tallgrass prairie, the ability to flexibly alter allocation to growth, reproduction, and defense would be expected to help maximize fitness (Bazzaz et al. 1987). It is important to increase our understanding of the link between environment and plant life history since, over time, widespread alterations in life history in response to environmental pressures can cause changes in population and community dynamics.

In tallgrass prairie, bison's preferential grazing of grasses has been shown to increase overall plant diversity vis-à-vis ungrazed prairies, with most of the additional species being forbs (Collins et al. 1998; Hartnett et al. 1996). Although grasses are responsible for the majority of annual net primary productivity in tallgrass prairie, forbs comprise the majority of the ecosystem's floristic diversity (Towne 2002). The mechanisms behind this promotion of forb diversity by bison, however, are not yet fully understood. Two proposed explanations include the Habitat Heterogeneity Hypothesis and the Competitive Release Hypothesis. Particularly when not over-stocked, bison have been shown to increase habitat heterogeneity, which, according to the niche diversity hypothesis, would help promote species diversity in bison-grazed prairie (Harnett et al. 1996; Knapp et al. 1999). When large grazers such as bison are removed, grass cover typically increases, forming a contrastingly homogeneous landscape that, in accordance with niche theory, contains fewer species (Eby et al 2014). Thus, the Habitat Heterogeneity Hypothesis posits that the increase in forb diversity and cover is due primarily to the increase in heterogeneity caused by large grazers and not to increases in forb performance (growth and reproduction). However, the increase in prairie grass cover in the absence of large grazers also seems to indicate that competitive pressure from grasses may inhibit the survival of many native prairie species when grazers are not present (Koerner & Collins 2013). Many

dominant prairie grasses have been shown to be resilient to grazing, sometimes to the point of practically benefitting (Coughenour 1985). They may adjust their growth and reproduction in response, but tend to survive even repeated instances of defoliation (N'Guessan & Hartnett 2011). However, in altering their growth and compensating for loss of tissue to grazers, their ability to compete for resources could potentially be altered. Thus, reduction of competitive pressure from grasses may also contribute to the survival and spread of species that might be unable to compete when bison are absent, leading to the observed increase in diversity. Thus, if the Competitive Release Hypothesis has merit, forb performance would be expected to be greater in habitats where bison are present due to reduced competitive pressure from grasses, and this increased performance at the individual level contributes to the overall increase in forb cover and diversity.

This study sought to test the latter hypothesis that release from competitive pressure from grasses may contribute to the increase in forb growth, reproduction, and cover associated with the presence of bison in tallgrass prairie. The specific objectives of this project were to 1) compare local light availability and vegetation density in habitats with and without bison, 2) compare plant performance in terms of growth and fecundity between individuals grown in habitats with and without bison, and 3) determine whether forbs respond to bison-induced alterations in habitat and resource availability by shifting biomass allocation patterns. I predicted that individuals grown in habitats where bison are present would generally be larger and more fecund than conspecifics grown in habitats without bison, but that these differences and other differences in life history would vary from species to species. Thus, by comparing the life history responses of individuals grown in bison-present and bison-absent habitats, I hope to unite

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our understanding of plant life history choices with the observed phenomenon of increased cover

and diversity of forb species in grazed prairie.

Methods

Site Description

This study was conducted at Konza Prairie Biological Station (KPBS), a 3487-hectare tallgrass prairie preserve which is jointly owned and run by the Nature Conservancy and Kansas State University. One of the six original NSF Long-Term Ecological Research Sites, KPBS is located in the Flint Hills ecoregion of Kansas (39°05′N, 96°35′W). The region is characterized by a continental climate with average monthly temperatures ranging from -2.7 to 26.6ºC. Average annual precipitation at KPBS is 835mm, approximately 75% of which falls during the growing season (Bark 1987). Between April 1 and October 31 of 2013, the year of this study, approximately 672mm of precipitation fell and temperatures ranged from -4.3 to 39.7ºC with an average of 19.4ºC (LTER dataset AWE012). KPBS is subdivided by watershed into numerous fire (burned every 1, 2, 4, or 20 years since 1972) and grazing management regimes (ungrazed, grazed by bison, grazed by cattle). Bison have been present in the native grazer treatments since 1987, allowing for the study of the long-term impacts of bison on plant communities (Knapp et al 1998). The vegetation of KPBS consists primarily of unplowed tallgrass prairie dominated by warm-season perennial grasses such as big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* Michx.), and Indiangrass (*Sorghastrum nutans* L.). Subdominant vegetation includes a diverse mix of forbs, cool-season grasses, and a few woody species. Over 576 species of vascular plant have been identified at KPBS from over 96 families, but over 40% of species belong to the families Poaceae, Asteraceae, Fabaceae, and Cyperaceae alone (Towne 2002). This study, conducted in 2013, sought to compare the growth and reproduction of plants in communities where bison were present with similar communities that lack bison. In this study, samples were taken from a total of three watersheds, all of which were

burned at 2-year intervals, most recently in spring 2012: N2A (bison-present treatment) and 2A and 2B (bison-absent treatment).

Species Description

Over 576 species of vascular plant have been identified in KPBS, of which over 75% are forbs (Towne 2002). From these, a total of six common, native, perennial forb species were chosen for this study as representatives of two of the most species-rich forb families found in tallgrass prairie: Asteraceae and Fabaceae. None of the species chosen for this study are considered palatable to large ungulate grazers. *Ambrosia psilostachya* DC., *Artemisia ludoviciana* Nutt., *Vernonia baldwinii* Torr., *and Solidago canadensis* L. are all rhizomatous representatives of Asteraceae. The rhizomatous *Baptisia australis* (L.) R. Br. and non-rhizomatous *Psoralidium tenuiflorum* (Pursh) Rydb. are both members of Fabaceae and are typically found in rocky upland or hillside prairies. They bloom April-June and are primarily insect-pollinated. *Ambrosia psilostachya* and *Artemisia ludoviciana* are both widespread in open prairies and primarily wind-pollinated, blooming August-October.   *Solidago canadensis* is most common in lowland sites, is primarily insect-pollinated, and blooms August-October. *Vernonia baldwinii*, also primarily insect-pollinated, is widespread in open prairies and blooms July-September.

Field Sampling

For each species, six naturally-occurring populations on similar terrain were located for sampling, three in the bison-present treatment and three in the bison-absent treatment. Within each population, a randomly-placed transect was used to select twelve individuals at randomly-chosen intervals of at least 2m. Thus, a total of 72 individuals of each species were randomly chosen for use in this study (36 in bison-present habitats and 36 in bison-absent habitats). The

placement of a transect for any one species did not affect the placement of transects for any other species. All individuals in the bison-present treatment were located in watershed N2A, but the plants sampled in the bison-absent treatment were split between the watersheds 2A and 2B at KPBS. Each individual was marked with a flag and metal tag in early May and followed throughout the growing season until it reached peak flower. An individual was defined as a single ramet for *A. psilostachya*, *A. ludoviciana*, *S. canadensis*, and *V. baldwinii*. For *B. australis* and *P. tenuiflorum*, an individual was defined as the marked stem and all living connected stems. If a marked individual died (or senesced prematurely), the nearest conspecific was chosen as a replacement and the death was noted. No signs of bison herbivory were observed on any individuals marked for use in this study.

Individuals were harvested when they reached peak flower or, in the case of vegetative individuals, when all neighboring individuals were at peak flower and no signs of reproductive development were discernible. The determination of when a reproductive individual was considered to be in peak flower varied according to species. For the anemochorous species *A. ludoviciana*, *S. canadensis*, and *V. baldwini*, individuals were considered at peak flower when all (or nearly all) flowers had reached full size but before the earliest-developing flowers released any propagules to the wind. *Ambrosia psilostachya* was considered at peak flower when all male and female flowers had reached full size. Since the fruits of *B. australis* and *P. tenuiflorum* are much heavier than the flowers, those species were considered to be in peak flower when all (or nearly all) flowers had developed into mature fruit. Whether each harvested individual was reproductive or vegetative was recorded. Since it is nonclonal, *P. tenuiflorum* was harvested by clipping stems at soil level, but all other species were excavated in order to collect underground vegetative reproductive structures. Extracting all root biomass was impractical in Konza's

rocky, clay-rich soil, but every effort was made to remove all rhizomes associated with each chosen individual. Ultimately, 29-36 individuals per treatment were harvested for each species (Table 1.1).

Plant Size

Plant size was measured in three ways: plant height, total aboveground biomass, and number of leaves or nodes. Each individual plant's height was measured to the nearest 0.5cm in the field prior to harvest at peak flower, or, for vegetative individuals, after all neighboring conspecifics had reached peak flower. Total aboveground biomass was determined in grams as the sum of the dry weights of all aboveground parts. Leaf or node number was determined by counting the number of nodes and living leaves as tissues were separated during dissection. One-way ANOVA was used to test for significant differences in height, total aboveground biomass, and number of leaves and nodes between bison-present and bison-absent environments for individuals of each species.

Biomass Allocation

After harvest, the aboveground portions of each plant were dissected into three main functional components: growth/support (stems), photosynthesis (leaves), and sexual reproductive structures (including flowers, bracts, and some peduncles/rachises). Only live tissues were retained for analysis. All parts of the plant were then oven-dried at 60º C for at least 72 hours, then weighed to the nearest 0.001g using a Mettler AE 100 scale immediately upon removal from the drying oven. Since herbivorous insects consumed a substantial quantity of the flowers and developing fruits of *B. australis*, making it impossible to determine the true weight of sexual reproductive material produced, the mass of floral stems (rachis/peduncle) was used as an approximation of reproductive biomass for all individuals of those species. The number of

flowers or fruits (or floral nodes in the case of *B. australis*) produced by each individual was also determined during dissection as an estimate of potential fecundity for each species except *S. canadensis*. Herbivorous insects also consumed many flowers of *P. tenuiflorum*, and only non-damaged fruits and flowers were counted for this species since that represents a more accurate estimate of functional fecundity than a count that included unviable flowers or fruit, and any potential bison-mediated differences in insect herbivory would be relevant to the survival and success of plant species. For each individual, all parts for each functional component were weighed together. Percent allocation to any given function was determined by dividing the mass of structures devoted to that function by total aboveground biomass for each individual. The stem:leaf ratio was also calculated by dividing the mass of an individual's stems by the mass of its leaves. One-way ANOVA was used to determine whether percent allocation to any one function, or stem:leaf ratio differed for individuals of each species between bison-present and bison-absent habitats for individuals of each species. For the percentage values, the test was run using a beta-distribution.

Of the five rhizomatous species studied, only three species had rhizomes that were sufficiently developed by time of harvest for analysis: *B. australis*, *S. canadensis*, and *V. baldwinii*. For each species, all developing rhizomes associated with each harvested individual were counted, excised, and collected. The rhizomes for each individual were then oven-dried at 60º C for at least 72 hours, then collectively weighed to the nearest 0.001g using a Mettler AE 100 scale immediately upon removal from the drying oven to attain the total mass of rhizomes per individual. The ratio of rhizome biomass to total aboveground biomass was calculated for each individual as an assessment of proportional allocation to vegetative reproduction. One-way ANOVA assuming a beta-distribution was used to determine whether proportional allocation to

vegetative reproduction differed for individuals of each species between bison-present and bison-absent habitats for individuals of each species.

Habitat Characterization

In order to better understand the differences between ungrazed and bison-grazed prairie habitats, aspects of the vegetation surrounding each individual such as vegetation density, light interception, canopy height, and ground cover were measured.

Vegetation density was estimated by measuring disk settling height (cm) of a pasture disk meter at 10 randomly-chosen locations near each transect during peak overall biomass in August. Pasture disk meters are a common non-destructive method of measuring vegetation density since there is typically a strong positive linear relationship between disk settling height and vegetation density in grassland communities (Bransby & Tainton 1997; Karl & Nicholson 1987; Sharrow 1984). In the absence of a calibration equation

Canopy height was determined as the average height of stems of neighboring individuals near each marked individual, to the nearest 5cm (not measured for *P. tenuiflorum*).

An AccuPAR LP-80 ceptometer (Decagon Devices, Pullman, WA) was used to measure photosynthetically active radiation ($\mu mol \cdot m^{-2} \cdot s^{-1}$) above the canopy (ambient), at the top of the sampled individual, and at ground-level near each marked individual (but outside of the shade of the individual itself). For each plant, light was measured five times at each of those three positions. The light available to each plant sampled could thus be quantified by calculating the average percentage of ambient light available at the top of the plant and at ground-level. All light measurements were taken within an hour of solar noon on clear days.

Percent canopy cover and diversity of neighbors was measured within a 0.5-m^2 plot centered around each marked individual. Percent cover of forbs, grasses, shrubs, conspecifics

(including the individual studied), and bare ground were estimated using a modified Daubenmire method. For each measurement, canopy cover was determined to be closest to the midpoint of any of 7 classes: 0-1%, 1-5%, 5-25%, 25-50%, 50-75%, 75-95%, or 95-100%. Diversity of forbs and shrubs was also estimated within each plot, but grass diversity was not measured due to the difficulty of identifying vegetative grass tillers.

One-way ANOVA was used to determine whether percent light availability, canopy height, non-graminoid plant species richness, vegetation density (settling height), or percent canopy cover were significantly different between bison-present and bison-absent habitats for individuals of each species. For the percentage values, the test was run using a beta-distribution.

Results

Ambrosia psilostachya

Average size of individuals of *A. psilostachya* was significantly different between bison-present and bison-absent habitats according to some measures. Total aboveground biomass of individuals in bison-present habitats was significantly greater (p<0.050; Figure 1.1). On average, individuals of *A. psilostachya* in bison-present habitats were significantly shorter than in bison-absent habitats (p=0.021; Figure 1.2). There was no significant difference in number of leaves (p=0.162) or leaf nodes (p=0.193) between bison-present and bison-absent areas (Figure 1.3). A significantly lower (p=0.003) percentage of marked individuals died prior to the end of the season in bison-present habitats than in bison-absent habitats.

There were some differences in vegetative growth between bison-present and bison-absent habitats for *A. psilostachya*. The total mass produced per individual of leaves (p=0.022) was significantly greater in bison-present habitats, but mass of stems was not significantly different (p=0.243; Figure 1.1). Average percent allocation of aboveground biomass to leaves (p=0.011) was significantly higher and percent allocation to stem (p<0.001) was significantly lower in bison-present habitats (Figure 1.4). Stem-to-leaf ratio was not significantly different in habitats where bison were present (p=0.142; Table 1.1).

Sexual reproduction differed somewhat between bison-present and bison-absent habitats for *A. psilostachya*. More individuals produced flowers in bison-present habitats than in bison-absent habitats, but the difference was not significant (p=0.068; Table 1.1). Average number (p=0.019; Figure 1.3) and total mass (p=0.010; Figure 1.1) of male flowers produced per individual were both significantly greater in bison-present habitats. However, average number (p=0.067; Figure 1.3) and total mass (p=0.092; Figure 1.1) of female flowers produced per

individual, though both greater in bison-present habitats, were not significantly different. Sexual reproductive effort, measured as the percentage of aboveground biomass allocated to sexual reproduction, was significantly greater (p=0.015; Figure 1.4) in habitats where bison were present.

The environments around the individuals of *A. psilostachya* studied differed significantly in some measures between bison-present and bison-absent habitats. The percentage of ambient light available at the top of individuals of *A. psilostachya* (p<0.001) and at ground-level near individuals of *A. psilostachya* (p<0.001) were both significantly higher in bison-present than in bison-absent habitats (Figure 1.5). Average height of the canopy near individuals of *A. psilostachya* was significantly shorter in bison-present habitats (p<0.001; Figure 1.2). Average vegetation density (disk settling height) was significantly lower (p<0.001) and non-grass diversity was significantly higher (p<0.001) in habitats where bison were present (Table 1.2). Average percent cover of conspecifics (p<0.001), all forbs (p<0.001), and bare ground (p<0.001) were all significantly higher in bison-present habitats; shrub and grass cover were not significantly different (Figure 1.6).

Artemisia ludoviciana

No measures of plant size or biomass allocation were significantly different between bison-present and bison-absent habitats for *A. ludoviciana* (Figures 1.7-9; Table 1.1).

Significantly more individuals of *A. ludoviciana* flowered (p=0.035; Table 1.1) in bison-present habitats than in bison-absent habitats; no other measures of sexual reproduction were significantly different. Average number of flowers produced per individual of *A. ludoviciana* was greater in bison-present areas, but the difference was not significant (p=.068; Figure 1.9).

The environments around the individuals of *A. ludoviciana* studied differed significantly in some measures between bison-present and bison-absent habitats. The percentage of ambient light available at the top of individuals of *A. ludoviciana* (p<0.001) and at ground level near individuals of *A. ludoviciana* (p<0.001) were both significantly higher in bison-present than in bison-absent habitats (Figure 1.11). Average height of the canopy near individuals of *A. ludoviciana* was significantly shorter in bison-present habitats (p<0.001; Figure 1.8). Average vegetation density (disk settling height) was significantly lower (p<0.001) and non-grass diversity was significantly higher (p<0.001) in habitats where bison were present (Table 1.2). Average percent cover of forbs (p=0.002) and bare ground (p=0.014) were significantly higher in bison-present habitats but shrub cover (p=0.012) was significantly lower. Grass cover was higher on average in bison-absent habitats, but the difference was not significant (p=0.064; Figure 1.12).

Baptisia australis

On average, individuals of *B. australis* were significantly larger in bison-present habitats than in bison-absent ones according to all measures of plant size used. Both average aboveground individual biomass (p<0.001; Figure 1.13) and height (cm) (p<0.001; 1.14) were significantly greater in bison-present habitats. Average number of living leaves (p<0.001) and leafing nodes produced (p<0.001) per individual were both significantly higher in bison-present habitats (Figure 1.15). One marked individual died prior to the end of the season in bison-absent habitat; no premature deaths were recorded in bison-present habitats.

There were some differences in vegetative growth between bison-present and bison-absent habitats. Average mass produced per individual of stems (p<0.001) and leaves (p<0.001) were significantly greater in bison-present habitats. However, allocation to stems (p=0.132) and

leaves (p=0.829) and stem:leaf ratio (p=0.255; Table 1.1) did not differ significantly between bison-present and bison-absent habitats for individuals of *B. australis* (Figure 1.16). On average, a significantly greater percentage of leaves produced by an individual were left undamaged by insects in bison-present habitats (40.6%±3.1) than in bison-absent habitats (20.1%±2.4; p<0.001).

All measures of sexual reproduction showed significantly higher output for *B. australis* in bison-present habitats. Significantly more individuals flowered when bison were present (p<0.001; Table 1.1), and, due in part to insect herbivory, no seeds were produced in bison-absent habitats. Significantly more flowers (p<0.001) and seeds (p=0.036) were produced per plant in bison-present habitats (Figure 1.15). Average mass of seeds (p<0.001) and rachises (p<0.001) produced per individual were both significantly greater in bison-present habitats (Figure1.13). Even controlling for the effects of tissue loss due to insect herbivory by using only the mass of rachises, average percent allocation of aboveground biomass to sexual reproduction (p=0.011) was significantly greater in bison-present habitats (Figure 1.16). Since all fruits and flowers in bison-absent habitats were at least partially to entirely consumed by herbivores but many in bison-present habitats were untouched, including the masses of fruits and other floral parts in the calculation of sexual reproductive allocation would only increase the apparent disparity between habitats.

Vegetative reproduction was not consistently different between habitats. Individuals in bison-present habitats produced significantly more rhizomes on average than individuals in bison-absent habitats (p=0.020; Figure 1.15), but neither average total mass (g) of rhizomes per individual (p=0.690; Figure 1.13) nor average proportional allocation of biomass to rhizomes (p=0.089; Figure 1.17) were significantly different between habitats.

The environments encountered by the individuals of *B. australis* studied were significantly different between bison-present and bison-absent habitats. The percentage of ambient light available at the top of individuals of *B. australis* (p<0.001) and at ground level near individuals of *B. australis* (p<0.001) were both significantly higher in bison-present than in bison-absent habitats (Figure 1.18). Average height of the canopy near individuals of *B. australis* was significantly shorter in bison-present habitats (p=0.006; Figure 1.14). Average vegetation density (disk settling height) was significantly lower (p<0.001) and non-grass diversity was significantly higher (p<0.001) in habitats where bison were present (Table 1.2). Average percent cover of conspecifics (p<0.001), all forbs (p<0.001), and bare ground (p<0.001) were all significantly higher in bison-present habitats whereas grass cover (p=0.002) was significantly lower; shrub cover was not significantly different (p=0.459; Figure 1.19).

Psoralidium tenuiflorum

No measures of overall plant size were significantly different for *P. tenuiflorum* between bison-present and bison-absent habitats (Figure 1.20-22). Average height was greater in bison-absent habitats, but the difference was marginally not significant (p=0.053; Figure 1.22). No marked individuals died prematurely in either habitat.

On average, individuals of *P. tenuiflorum* allocated a significantly smaller percentage of aboveground biomass to stem (p<0.001; Figure 1.23) in bison-present habitats, but allocation to leaves (p=0.307) and stem:leaf ratio (p=0.325; Table 1.1) were not significantly different, nor was average mass of leaves (p=0.618) or stems (p=0.728; Figure 1.20) produced by individuals.

There were some differences in sexual reproduction between bison-present and bison-absent habitats. Average mass of sexual reproductive parts (p=0.020; Figure 1.20) and average percentage of individual biomass allocated to sexual reproduction (p<0.001; Figure 1.23) using

total mass of all floral reproductive organs (rachis, fruit, and other floral parts) were both significantly greater in bison-present habitats than in bison-absent habitats. The proportion of flowering individuals (p=0.402; Table 1.1) and average number of fruits produced per individual (p=0.230) were not significantly different.

The environments encountered by the individuals of *P. tenuiflorum* studied were significantly different between bison-present and bison-absent habitats. The percentage of ambient light available at ground level near individuals of *P. tenuiflorum* (p<0.001) was significantly higher in bison-present than in bison-absent habitats, but light availability at the top of individuals was not significantly different (p=0.286; Figure 1.24). Average height of the canopy near individuals of *P. tenuiflorum* was not measured. Average vegetation density (disk settling height) was significantly lower (p<0.001) and non-grass diversity was significantly higher (p<0.001) in habitats where bison were present (Table 1.2). Average percent cover of bare ground (p<0.001) was significantly higher in bison-present habitats whereas grass cover (p<0.001; Figure 1.25) was significantly lower.

Solidago canadensis

Individuals of *S. canadensis* were, on average, significantly larger in habitats where bison were present. Total aboveground biomass of individuals in bison-present habitats was significantly greater on average (p=0.001; Figure 1.26), but height was not significantly different (p=0.209; Figure 1.27). On average, individuals in bison-present habitats had significantly more living leaves (p<0.001) and produced significantly more leafing nodes on the main stem (p=0.019; Figure 1.28). Three marked individuals in bison-absent habitats died prior to the end of the season; no marked individuals died in bison-present habitats.

There were some differences in vegetative growth between bison-present and bison-absent habitats. The total mass produced per individual of leaves (p=0.002) and of stems (p=0.010) were both significantly greater in bison-present habitats (Figure 1.26). Individuals in bison-present habitats allocated a significantly lower average percentage of aboveground biomass to stem (p<0.001), but allocation to leaves (p=0.952) and stem:leaf ratio (p=0.084; Table 1.1) were not significantly different (Figure 1.29).

Sexual reproduction was higher overall for *S. canadensis* in bison-present habitats. Significantly more individuals flowered in bison-present habitats (p=0.004; Table 1.1). On average, individuals allocated a greater percentage of their aboveground biomass to sexual reproduction (p<0.001; Figure 1.29) and produced a greater total mass of floral reproductive organs (p<0.001; Figure 1.26) in habitats where bison were present.

Vegetative reproduction was not consistently different between habitats. Neither number (p=0.685; Figure 1.28) nor total mass (g) (p=0.506; Figure 1.26) of rhizomes per individual were significantly different between habitats, but proportional allocation of biomass to vegetative reproduction was significantly lower in individuals grown in bison-present habitats (p=0.016; Figure 1.17).

The environments encountered by the individuals of *S. canadensis* studied were significantly different between bison-present and bison-absent habitats. The percentage of ambient light at ground level near individuals of *S. canadensis* (p<0.001) was significantly higher in bison-present than in bison-absent habitats, but there was no significant difference in percentage of ambient light available at the top of individuals (p=0.376; Figure 1.30). Average height of the canopy near individuals of *S. canadensis* was significantly shorter (p<0.001) in habitats where bison were present (Figure 1.27). Average vegetation density (disk settling

height) was significantly lower (p<0.001) and non-grass diversity was significantly higher (p<0.001) in habitats where bison were present (Table 1.2). Average percent cover of bare ground (p<0.001) and of forbs (p=0.003) were significantly higher in bison-present habitats whereas grass cover (p=0.006; Figure 1.31) was significantly lower.

Vernonia baldwinii

Individuals of *V. baldwinii* were, on average, significantly larger in habitats where bison were present. Total aboveground biomass of individuals in bison-present habitats was significantly greater (p<0.001; Figure 1.32) in bison-present habitats. There was no significant difference in height of individuals of *V. baldwinii* between bison-present and bison-absent habitats (Figure 1.33). On average, individuals in bison-present habitats had significantly more living leaves (p<0.001) and produced significantly more leafing nodes (p<0.001; Figure 1.34). The total mass produced per individual of leaves (p<0.001) and of stems (p<0.001) were both significantly greater in bison-present habitats (Figure 1.32). Five marked individuals died prior to the end of the season in bison-absent habitats, whereas only one premature death was recorded in bison-present habitats.

Individuals in bison-present habitats allocated a significantly lower average percentage of aboveground biomass to stem (p=0.001), but allocation to leaves (p=0.480; Figure 1.35) and stem:leaf ratio (p=0.207; Table 1.1) were not significantly different. Individuals in bison-present habitats lost a significantly lower (22.1%±2.2; p=0.007) percentage of their leaves on average than individuals in bison-absent habitats (31.4%±2.5).

In habitats where bison were present, sexual reproduction was significantly greater. Significantly more individuals produced flowers (p<0.001; Table 1.1) in bison-present habitats, and average mass of floral reproductive parts per individual (p<0.001; Figure 1.32) and number

of flowers per individual (p<0.001; Figure 1.34) were both significantly greater in bison-present habitats. No flowers became mature enough to produce seeds in bison-absent habitats, whereas at least 1013 flowers matured to the point of seed production in bison-present habitats. On average, individuals in bison-present habitats allocated a significantly greater percentage of aboveground biomass to floral reproductive parts (p<0.001; Figure 1.35).

Vegetative reproduction was not consistently different between habitats. Individuals in bison-present habitats produced significantly more rhizomes on average than individuals in bison-absent habitats (p<0.001; Figure 1.34), but average total mass (g) of rhizomes per individual (p=0.680; Figure 1.32) was not significantly different (p=0.680; Figure 1.32). Average proportional allocation of biomass to vegetative reproduction was lower in bison-present habitats, but the difference was only marginally significant (p=0.059; Figure 1.17).

The environments encountered by the individuals of *V. baldwinii* studied were significantly different between bison-present and bison-absent habitats. The percentage of ambient light at ground level near individuals of *V. baldwinii* (p<0.001) was significantly higher in bison-present than in bison-absent habitats, but there was no significant difference in percentage of ambient light available at the top of individuals (p=0.078; Figure 1.36). Average height of the canopy near individuals of *V. baldwinii* was significantly shorter (p<0.001; Figure 1.33) in habitats where bison were present. Average vegetation density (disk settling height) was significantly lower (p<0.001) and non-grass diversity was significantly higher (p<0.001) in habitats where bison were present (Table 1.2). Average percent cover of bare ground (p<0.001) and of forbs (p<0.001) were significantly higher in bison-present habitats whereas grass cover (p<0.001; Figure 1.37) was significantly lower.

Discussion

Habitat Differences

Competition for light appears to be significantly reduced in habitats with bison. The percentage of ambient light available at ground-level was consistently significantly greater in habitats with bison, indicating greater overall potential light availability for individuals. The percentage of ambient light available at the top of the individual studied was significantly greater in habitats with bison for three out of the six species studied, indicating much stronger competition for light in habitats without bison. The three species for which top-of-plant light availability was not significantly different tend to be taller in stature, so the lack of significant difference for this measurement is due their being taller than or similar in height to the surrounding canopy rather than a true lack of difference in the light environment for those species. Neighborhood vegetation density and canopy height were both consistently significantly lower in habitats with bison, and this lower height and density of surrounding vegetation help explain the difference in light availability between habitats. Since light is the ultimate source of energy for plant growth and survival, the strongly diminished availability of this critical resource in habitats without bison would be expected to have a large effect on the growth of plants in the community.

Habitats with bison also showed changes in ground cover in the local neighborhood of the individuals studied. Non-graminoid (forbs and few shrubs) diversity was consistently significantly higher in habitats with bison than in habitats without large grazers. In habitats where bison were present, cover of non-graminoids was significantly greater for five out of six species, cover of grass was significantly lower for four out of six species, and availability of bare ground was consistently higher. The lack of difference in forb cover for *P. tenuiflorum* might be

partially due to the consistently large percentage of the local neighborhood sample area covered by individuals of that species rather than a true lack of difference in diversity between habitats. Cover of individuals of the species of interest in bison-present habitats was significantly greater for *A. psilostachya* and *B. australis*, probably due to a combination of higher forb densities and (particularly for *B. australis*) individuals of the species of interest being larger and more branched. Increased forb cover and diversity in habitats where bison are present is consistent with the findings of previous studies (Collins et al. 1998; Hartnett et al. 1996; Hickman et al. 2004). In high-density tallgrass prairie communities, lack of space can inhibit the germination, emergence, and survival of seeds and ramets, so greater availability of bare ground in habitats with bison means that there is more potential for the establishment of new individuals. The decrease in grass cover where bison are present, particularly coupled with increases in forb cover and bare ground, indicate a difference in community structure between the two prairie habitats: strongly grass-dominated without bison vs. more diverse and heterogeneous in the presence of bison.

Taken together, the differences in light, canopy height, vegetation density and composition, and ground cover paint the picture of two distinctly different aboveground environments for forbs. In the absence of bison, forbs compete predominantly with the strongly-dominant grasses, which significantly decrease the availability of light and bare ground. Contrastingly, grasses are less dominant in habitats where bison are present, so that forbs are more likely to be surrounded by a more diverse array of potentially competing neighbors and to experience less light- and space-limitation. This increased resource availability in bison-present habitats, if not coupled with compensating limitation of some other resource, could reasonably be expected to lead to increased growth and reproduction in forb species capable of such

plasticity. Though aspects of the belowground environment were not measured in this study, the

two habitats may also differ in nutrient availability, soil moisture, soil microbiota, and soil

temperature, but these differences would not generally be expected to decrease forb performance

in habitats with bison (Fahnestock & Knapp 1994; Frank & Groffman 1998; Hobbs 1996; Knapp

& Seastedt 1986; Knapp et al. 1999; Veen et al. 2014; Wilson et al. 2001).

Plant Growth and Reproduction

On average, forb size in habitats where bison were present was greater than or equivalent

to individual plant size in bison-absent habitats. For four out of six species, individual size was

significantly greater in bison-present habitats according to at least one measure. In bison-present

habitats, total aboveground biomass was significantly greater for four out of six species, as were

leaf and node number for three out of six. Since plants are modularly-constructed organisms, the

number of parts, particularly of leaves/nodes, is a biologically-relevant measure of plant size and

growth rate (Harper 1977). Increased growth, as measured by biomass or number of

leaves/nodes, in habitats where bison are present supports the hypothesis that release from

competition with grasses favors forb performance in habitats with bison. Height showed no

overall pattern: it was not significantly different for four species whereas individuals of *B.*

australis were significantly taller and of *A. psilostachya* significantly shorter in bison-present

habitats. Light limitation can cause plants to produce longer internodes, so the lack of a

consistent difference in height despite other evidence of reduced growth in habitats where bison

are absent helps support the hypothesis that light limitation may affect forb growth in ungrazed

prairie habitats (Dudley & Schmitt 1996; Harper 1977; Lockhart 1964). Two species (*A.*

ludoviciana and *P. tenuiflorum*) showed no significant differences in size; it is possible that these

species are less able to plastically alter their growth in ways measured by this study, face

equivalent levels of resource limitation in habitats with or without bison, or are less sensitive to the environmental differences between bison-grazed and ungrazed prairie habitats. Nevertheless, the fact that four species showed increased size in terms of biomass and/or module number in bison-present habitats despite not necessarily being taller provides evidence that resources, particularly light, may be more available in bison-grazed prairie than in ungrazed prairie.

At least one measure of sexual reproduction was greater in bison-present habitats for all six species. Individuals in bison-present habitats were significantly more likely to flower for all species except *P. tenuiflorum* (whose flowering did not differ significantly). At least one measure of sexual reproductive output was significantly greater in bison-present habitats for four out of six species: number of flowers was greater for 3 out of the 5 species for which numbers were available, and mass of reproductive structures produced per individual was greater for all species except *A. ludoviciana*. Production of male reproductive structures was greater in *A. psilostachya* in habitats where bison were present whereas female reproduction was not different. Number of flowers and mass of sexual reproductive structures can be interpreted as estimates of fecundity since they should increase allometrically with the number of seeds produced in the absence of mitigating factors such as seed predation. Sexual reproductive effort (percentage of individual biomass allocated to sexual reproduction) was significantly greater in bison-present habitats for all species except *A. ludoviciana*. Thus, not only were more forbs reproductive in bison-grazed habitats for most species studied, but they were also generally more fecund, resulting in much greater sexual reproductive output in habitats with bison.

Vegetative reproduction did not show a clear pattern of difference between habitats for any of the three species in which it was studied: *B. australis*, *S. canadensis*, and *V. baldwini*. Despite the fact that plants of each species were on average at least twice as large in habitats with

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bison, there was no significant difference in average total mass of rhizomes produced for any

species studied. Individuals of *S. canadensis* allocated a significantly greater proportion of total

biomass to vegetative reproduction in bison-absent habitats, but there was no significant

difference in allocation for the other two species. *Baptisia australis* and *Solidago canadensis*

produced more rhizomes in bison-present habitats, but average rhizome size must have been

reduced since there was no commensurate increase in total rhizome mass. Each rhizome is a

potential vegetative offspring (ramet), so producing a greater number of rhizomes could lead to

faster vegetative spread if ramet recruitment rates are equivalent (or greater) in grazed habitats.

Environmental factors, such as strong competition for space, may promote the enhancement or

maintenance of vegetative reproduction in ungrazed prairie more strongly than in grazed prairie,

leading to greater relative vegetative reproductive effort in ungrazed prairie. Seed recruitment in

tallgrass prairie is relatively rare, so vegetative reproduction is a very important mechanism of

population growth and maintenance in prairie habitats regardless of grazer habitats, and it might

be expected to be particularly critical in bison-absent prairie where light- and space-limited

conditions make the probability of successful recruitment from seed very low (Benson &

Hartnett 2006). If there is a trade-off between allocation to sexual and vegetative reproduction,

as has been proposed by some (Ronsheim & Bever 2000; Sutherland & Vickery 1988;

Thompson & Eckert 2004; Worley & Harder 1996), the increase in sexual reproduction in bison-

grazed habitats may have limited individual's ability to increase allocation to vegetative

reproduction, and vice versa for individuals in bison-absent habitats. The lack of plasticity in

total vegetative productive mass despite other changes in growth could indicate that vegetative

reproduction may be more affected by species-specific constraints than by environmental

pressures or changes in size. However, rhizome buds may not mature at the same time as

flowers and fruit in every species, and variation in rate of development could mean that this snapshot gave a skewed or incomplete picture of the true end-of-season rhizome production for some individuals. More studies of rhizome development and the factors regulating it are needed in order to better explain the observed lack in overall differences in vegetative reproduction between grazed and ungrazed habitats. It is particularly important to improve our understanding of the factors regulating vegetative reproduction, particularly if trade-offs with sexual reproduction are involved, since for many perennial prairie species it is the primary mode of reproduction (Benson et al. 2004). Since vegetative reproduction does not increase genetic diversity, populations which are overly reliant on this mode of propagation may be less able to respond to environmental change or, in extreme cases, to set seed due to scarcity of sufficiently unrelated pollen (Charpentier et al. 2000).

If release from competition contributes to the increase in forb cover and diversity in bison-grazed prairie, performance of individual forbs would be expected to be greater in bison-grazed prairie than in ungrazed prairie. This study found evidence of increased performance in all six species studied, though the species varied in strength and type of response. *Ambrosia psilostachya*, *Baptisia australis*, *Solidago canadensis*, and *Vernonia baldwinii* all showed significantly greater size and sexual reproduction in bison-grazed habitats according to most measures used, and vegetative reproduction was not reduced in bison-grazed habitats. *Ambrosia psilostachya* also demonstrated a significantly greater survival rate in habitats where bison were present. Aboveground size was not significantly different between habitats for *A. ludoviciana* and *P. tenuiflorum*, but at least one measure of sexual reproduction was significantly greater in prairie grazed by bison for those species. The removal of grass biomass by bison lessens the competitive ability of dominant grasses, decreases local neighborhood vegetation density, and

increases the availability of light (and potentially other resources), leading to greater forb growth and reproduction.

Aboveground Allocation Patterns

Five out of six species showed significant shifts in biomass allocation among aboveground organs. Four out of six species showed decreased allocation to stem and increased allocation to reproduction in bison-present habitats. *A. psilostachya* also showed increased allocation to leaf and to male reproduction in habitats where bison are present, but allocation to female reproduction was not different. One species, *B. australis*, showed greater allocation to sexual reproduction in bison-present habitats without any significant difference in stem allocation. Differences in stem:leaf ratio between habitats were not observed for any species. Thus, many species of forb are able to plastically alter their growth strategies in response to environmental pressures, which is not surprising since an ecosystem like tallgrass prairie that is marked by great inter-annual and within-season resource variability would be expected to select for plasticity, particularly in perennial species. Only *A. ludoviciana*, which also showed little plasticity in size or reproduction, showed no significant differences in allocation to any function.

Leaf allocation was consistent between habitats for five out of six species. Since leaves are the organs plant use to fix carbon for use to build and energetically maintain other plant parts, the lack of difference in leaf allocation between habitats may indicate that all individuals were maintaining the optimal leaf allocation required for survival of that species. Increasing allocation to leaves beyond this level may no longer be energetically favorable, perhaps because the respirational costs of maintaining additional layers of leaves may begin to outweigh the potential gain in photosynthesis due to the shading effect of upper leaves at a certain point. Some species, such as *V. baldwinii*, actively stabilized their allocation to leaves by dropping a

significantly greater percentage of their lower leaves in habitats without bison. Individuals of *A. psilostachya* allocated significantly less biomass to leaves in bison-absent habitats, perhaps indicating that these individuals were struggling to photosynthesize enough to even maintain leaf tissue in such a low-light habitat. This failure to maintain sufficient allocation to leaves may help explain the significant increase in individual mortality for *A. psilostachya* in ungrazed habitats. Thus, allocation of aboveground biomass to leaves may be more dictated by respirational needs and survival than by light availability for forbs in tallgrass prairie.

Since stem:leaf ratio was not significantly different between habitats for any species, the reduction in stem allocation observed in four of the species studied was likely related to increased allocation to sexual reproduction. As might be expected for plants in very light-limited herbaceous communities, individuals of *A. psilostachya* in bison-absent habitats showed signs that vertical growth was of enhanced importance, for stem allocation and height were both significantly greater, to the detriment of allocation to leaves and reproduction. In environments like the ungrazed habitat in this study where competition for light is heavy, individuals may need to allocate a greater proportion of biomass to stem in order to maintain vertical growth towards greater light availability higher in the (taller) canopy and avoid death from insufficient light. In higher-light environments, vertical growth is less important, enabling the plant to invest some of the energy that would have been allocated to stem in reproduction. *Baptisia australis* individuals in bison-present habitats showed greater allocation to sexual reproduction, but rachises comprised such a small percentage of overall biomass that any proportional change in allocation to stem (or leaves) could not be significantly different. Thus, for species that allocated biomass differently between the two habitats, there seemed to be a trade-off between allocation to stem

and to sexual reproduction, which is consistent with light limitation promoting stem allocation more in bison-absent habitats than in bison-present habitats.

Other Indirect Effects: Insects and Phenology

Though not the focus of this study, differences in phenology and insect damage between the two habitats appeared to contribute to some of the observed differences in performance. None of the areas used in this study had been burned since the previous growing season, so considerably more dead plant litter was present in the non-grazed habitats, which seemed to noticeably delay the growth and flowering of some species, particularly *B. australis* and *V. baldwinii,* in the ungrazed prairie. Such differences in phenology could be caused by delayed soil warming due to the built-up biomass's blocking of sunlight in addition to lower light resource availability slowing plant growth rate (Knapp & Seastedt 1986). The blooming seasons of *A. psilostachya*, *A. ludoviciana*, and *S. canadensis* were more protracted in both habitats and any phenological delays had less obvious consequences. The delayed phenology observed in some of the species studied is further evidence of how the differences in vegetation density between grazed and ungrazed prairie can lead to differences in plant growth and reproductive outcomes.

Delayed flowering proved to be particularly significant for *B. australis* since an outbreak of *Epicauta* sp. (blister beetles) a few weeks into the growing season consumed all flowers, flower buds, fruits below a certain size, and immature leaves. Since *B. australis* individuals in bison-grazed habitats had few immature leaves and had bloomed earlier, the majority of their leaves and many fruits were left uneaten by *Epicauta* sp. However, due to the delay in phenology, individuals in ungrazed habitats had more immature leaves and no fruits too mature to be eaten by *Epicauta* sp., so all flowers and fruits and a significantly greater proportion of

leaves were consumed by *Epicauta* sp. The observed difference in sexual reproduction between habitats for *B. australis* cannot be entirely attributed to the effects of insect herbivores, however, since significantly more flowers were produced in bison-grazed habitats and floral reproductive allocation was higher even when only rachis masses (rachises were uneaten by *Epicauta* sp.) were considered. Thus, the differences in size and sexual reproduction between habitats for *B. australis* were magnified by a combination of insect herbivory and differences in phenology. Such outbreaks of *Epicauta* sp. herbivory are not an unusual occurrence for *B. australis* (Evans 1990).

Individuals of *V. baldwinii* in bison-present habitats matured and began to develop flowers earlier than individuals in ungrazed habitats. Since any *V. baldwinii* floral buds that had not opened before a certain warm, dry period in July failed to mature any further in either habitat, no seeds or mature flowers were produced by individuals in bison-absent habitats due to their delayed phenology.

Tallgrass prairies are complex ecosystems characterized by a complex network of interactions between species within and among trophic levels. The presence of large grazers has been shown to have a significant impact on other types of organism within the tallgrass prairie (Joern 2005; Moran 2014; Powell 2006), so it is not surprising that some of the effects of bison observed in this study were mediated by interactions with other organisms. Many other studies have found that plant responses to the common major disturbances of fire and grazing in tallgrass prairie are often mediated indirectly by other biotic interactioins (Blue et al. 2011; Hajny et al. 2011; Wilson et al. 2001) or by weather conditions (Fahnestock & Knapp 1994; Fay et al. 2003; La Pierre et al. 2011,).

Conclusion

In summary, this study found evidence supporting the hypothesis that release from competition with grasses contributes to the increased forb abundance in bison-grazed tallgrass prairie. This study established that bison significantly increase light availability and decrease local vegetation density compared to ungrazed prairie, and that this increased availability of aboveground resources is associated with increases in the performance of forb individuals (for all six species studied) and shifts in biomass allocation (for five out of six species studied). Such enhancements in growth and reproduction at the individual level are important to understand since, over time, they can lead to increases in cover and population size for that species. In habitats where reproduction and growth of individuals are strongly inhibited by environmental conditions, low fecundity or survivorship would be expected to cause populations to stagnate or decrease over time. Since the preservation of the floristic diversity of the highly endangered tallgrass prairie ecosystem is an important conservation issue, it is critical that we continue to increase our understanding of how management decisions like grazing lead to changes in species populations.

Table 1.1 All species: number of individuals sampled, percentage of sampled individuals flowering, percentage of marked individuals that died prior to the end of the season, and stem:leaf ratio compared between habitats with and without bison.

Stem:leaf ratio was calculated as the mass (g) of stems divided by the mass (g) of leaves for each individual.

Species	# of Individuals Sampled		% Flowering		% Died		Stem: Leaf Ratio (mean±SE)	
	Bison-Present	Bison-Absent	Bison-Present	Bison-Absent	Bison-Present	Bison-Absent	Bison-Present	Bison-Absent
A. psilostachya	35	32	97.1	81.3	14.3	50.0	1.64±1.60	5.06±1.67
A. ludoviciana	35	33	65.7	39.4	11.4	3.0	1.30±.09	1.32±.09
B. australis	29	31	86.2	29.0	0	3.2	.98±.14	1.20±.13
P. tenuiflorum	30	30	93.3	86.7	0	0	.90±.09	1.02±.09
S. canadensis	32	33	87.5	51.5	0	11.4	1.32±.17	1.74±.17
V. baldwinii	30	30	80.0	16.7	3.2	16.1	.77±.08	.92±.08

Figure 1.1 *Ambrosia psilostachya*: Mean (±SE) biomass (g) of vegetative and reproductive structures for individuals grown in habitats with or without bison.

An asterisk represents a significant ($\alpha=0.05$) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.

Figure 1.2 *Ambrosia psilostachya***: Mean (±SE) height (cm) of individuals and the surrounding neighborhood canopy in habitats with and without bison.**

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.

Figure 1.3 *Ambrosia psilostachya***: Mean (±SE) number of vegetative and reproductive structures per individual plant in habitats with and without bison.**

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.

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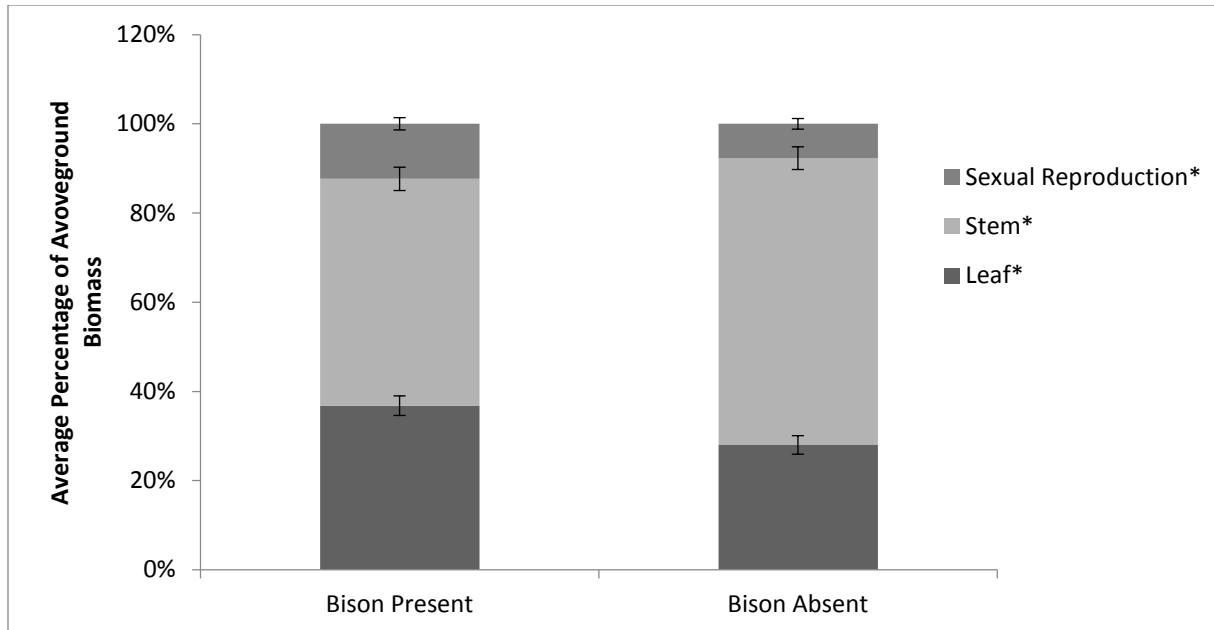
Figure 1.4 *Ambrosia psilostachya*: **Comparison of biomass allocation patterns (mean ± SE) between individuals grown in bison-present and bison-absent habitats.**

Biomass allocation to each function was calculated as total individual mass of structures devoted to that function divided by total individual biomass. An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
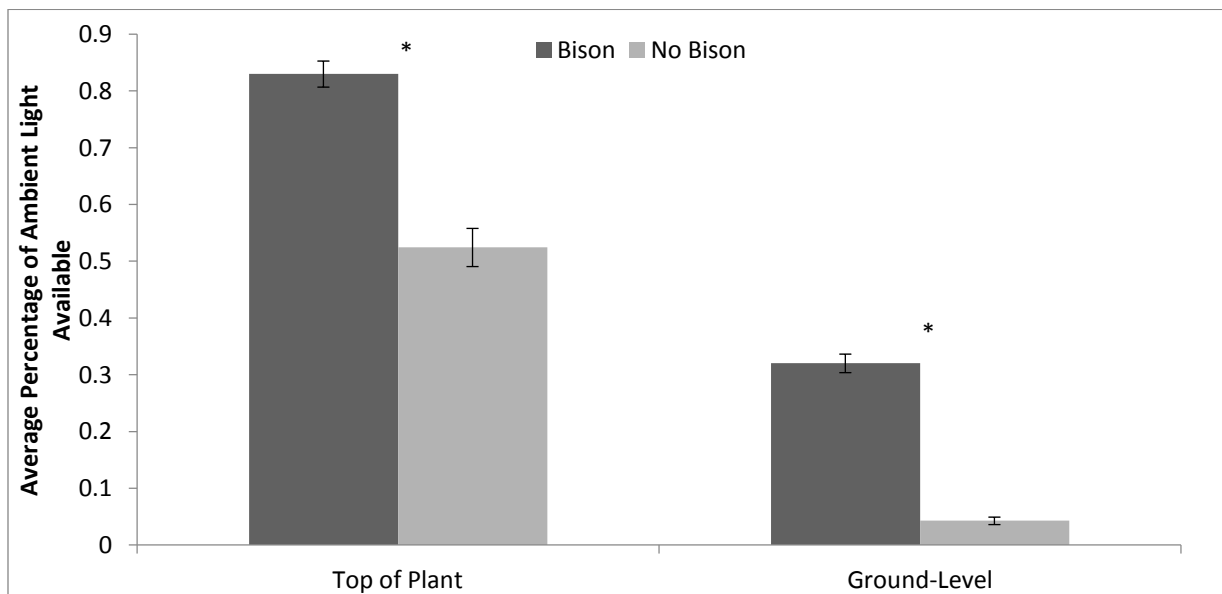
Figure 1.5 *Ambrosia psilostachya*: **Mean (±SE) percentage of ambient light available at the top of individuals and at soil-level for plants in habitats with and without bison.**

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.

Table 1.2 All species: Mean (±SE) species richness of non-graminoid neighbors and surrounding vegetation density.

Species richness per .5-m^2 plot was calculated by estimating the number of nongrass species present in a .5-m^2 plot centered around each individual plant sampled in this study. Species richness per transect was calculated as the total number of species found in all .5-m^2 plots in a single transect for a given study species. Average species richness per plot and per transect are both given here. Vegetation density was estimated using a pasture disc at a randomly-chosen point near the individuals studied of each species; the measurements given are for disk settling height (cm). All comparisons of neighbor species richness and of vegetation density between bison-present and bison-absent habitats were significant at the α=0.05 level.

	Non-graminoid Richness per Transect		Non-graminoid Richness per .5-m^2 plot		Vegetation Density (disk settling height, cm)	
	Bison-Present	Bison-Absent	Bison-Present	Bison-Absent	Bison-Present	Bison-Absent
A. psilostachya	24.3±2.3	12.0±3.0	7.6±0.3	3.1±0.3	8.3±0.9	24.5±0.9
A. ludoviciana	24.0±1.0	12.0±3.1	7.5±0.3	3.7±0.4	8.0±0.9	22.6±0.9
B. australis	26.3±1.2	15.1±2.6	8.4±0.4	4.9±0.4	8.0±0.6	16.2±0.6
P. tenuiflorum	21.0±1.5	11.7±0.7	9.4±0.4	5.4±0.4	6.9±1.1	23.9±1.1
S. canadensis	27.5±3.0	10±1.2	8.9±0.3	3.5±0.3	5.3±0.7	26.9±0.7
V. baldwinii	22.6±6.9	13.3±1.3	7.4±0.3	4.2±0.3	4.9±0.9	25.1±0.9

Figure 1.6 *Ambrosia psilostachya*: Mean (±SE) percent canopy cover within a 0.5-m^2 sample of vegetation surrounding individuals in habitats with and without bison.

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
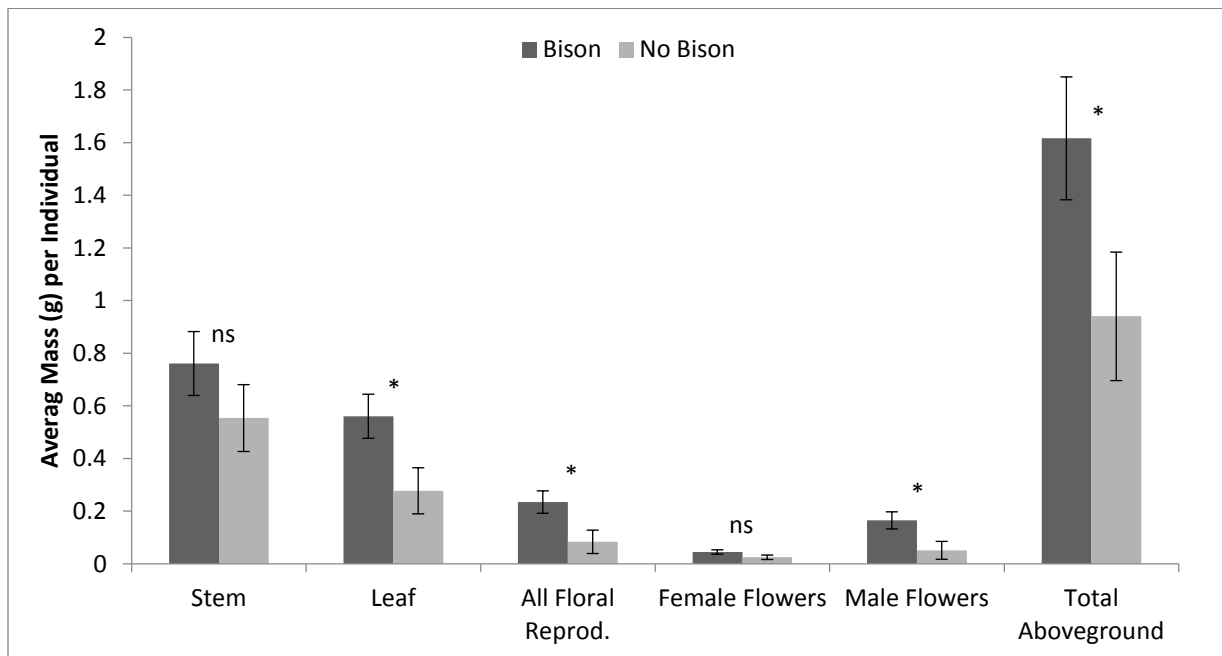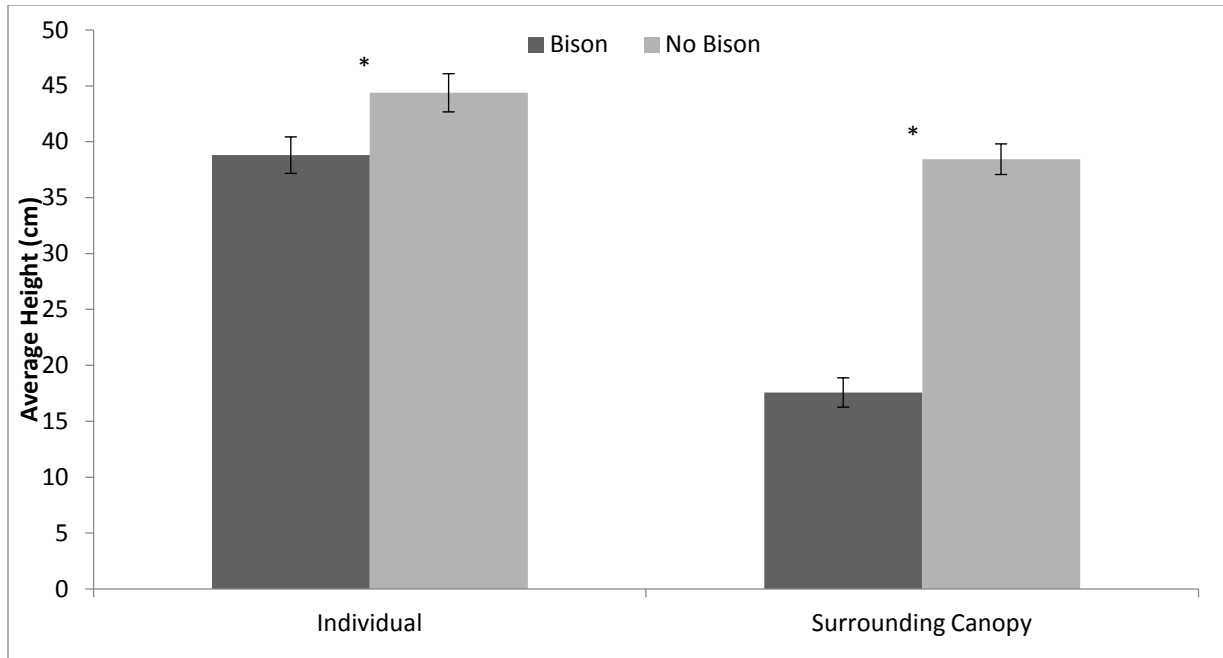
Figure 1.7 *Artemisia ludoviciana*: Mean (±SE) biomass (g) of vegetative and reproductive structures for individuals grown in habitats with or without bison.

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.

Figure 1.8 *Artemisia ludoviciana*: Mean (±SE) height (cm) of individuals and the surrounding neighborhood canopy in habitats with and without bison.

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.

**Figure 1.9** *Artemisia ludoviciana***: Mean (±SE) number of vegetative and reproductive structures per individual plant in habitats with and without bison.**

An asterisk represents a significant ($\alpha=0.05$) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
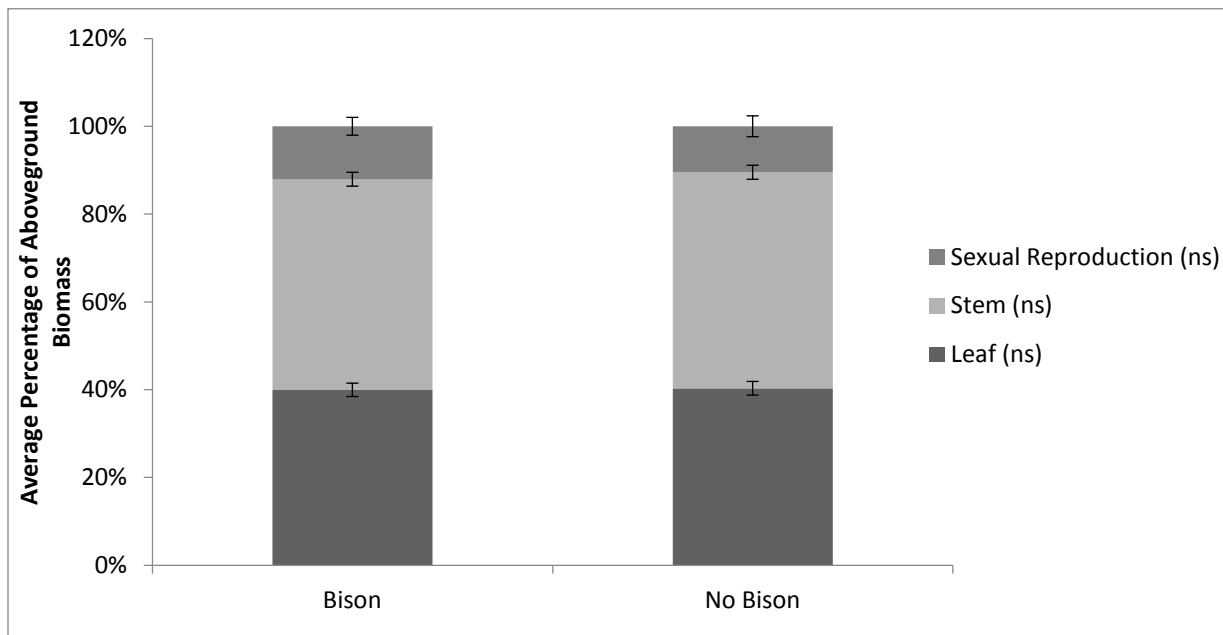
Figure 1.10 *Artemisia ludoviciana***: Comparison of biomass allocation patterns (mean ± SE) between individuals grown in bison-present and bison-absent habitats.**

Biomass allocation to each function was calculated as total individual mass of structures devoted to that function divided by total individual biomass. An asterisk represents a significant ($\alpha=0.05$) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.

Figure 1.11 *Artemisia ludoviciana***: Mean (±SE) percentage of ambient light available at the top of individuals and at soil-level for plants in habitats with and without bison.**

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
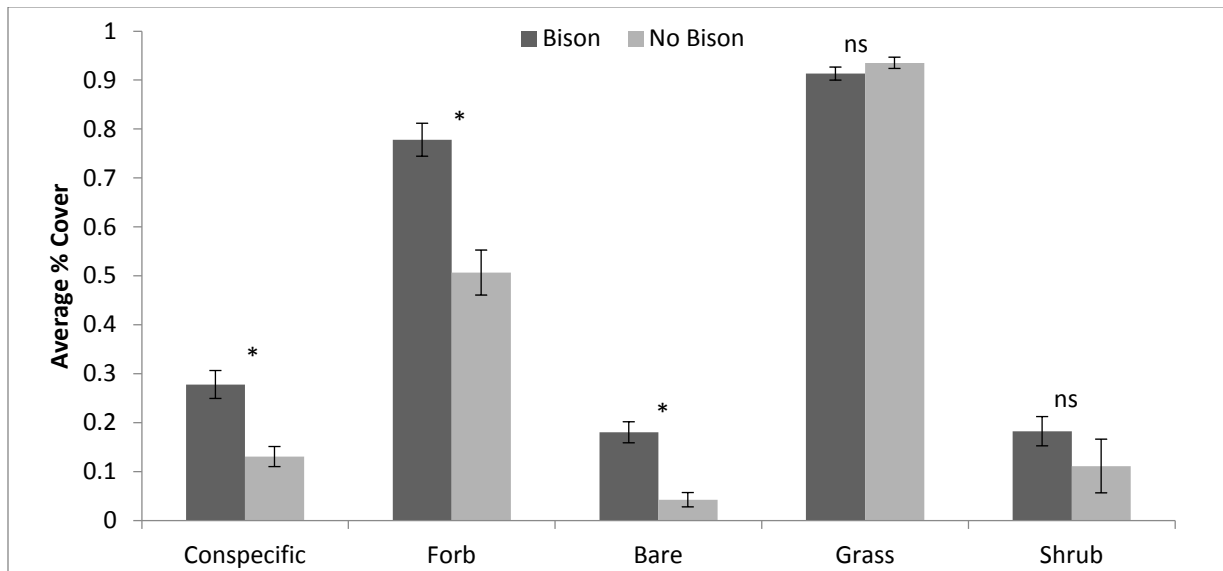

Figure 1.12 *Artemisia ludoviciana***: Mean (±SE) percent canopy cover within a 0.5-m^2 sample of vegetation surrounding individuals in habitats with and without bison.**

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.

Figure 1.13 *Baptisia australis*: Mean (±SE) biomass (g) of vegetative and reproductive structures for individuals grown in habitats with or without bison.

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.

Figure 1.14 *Baptisia australis*: Mean (±SE) height (cm) of individuals and the surrounding neighborhood canopy in habitats with and without bison.

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.

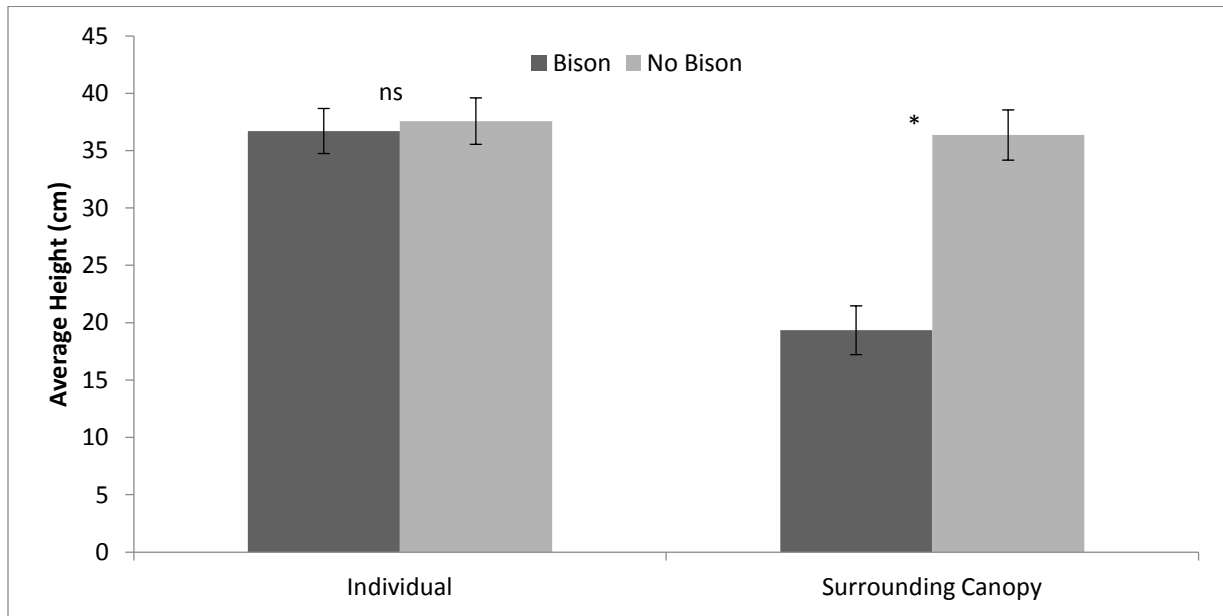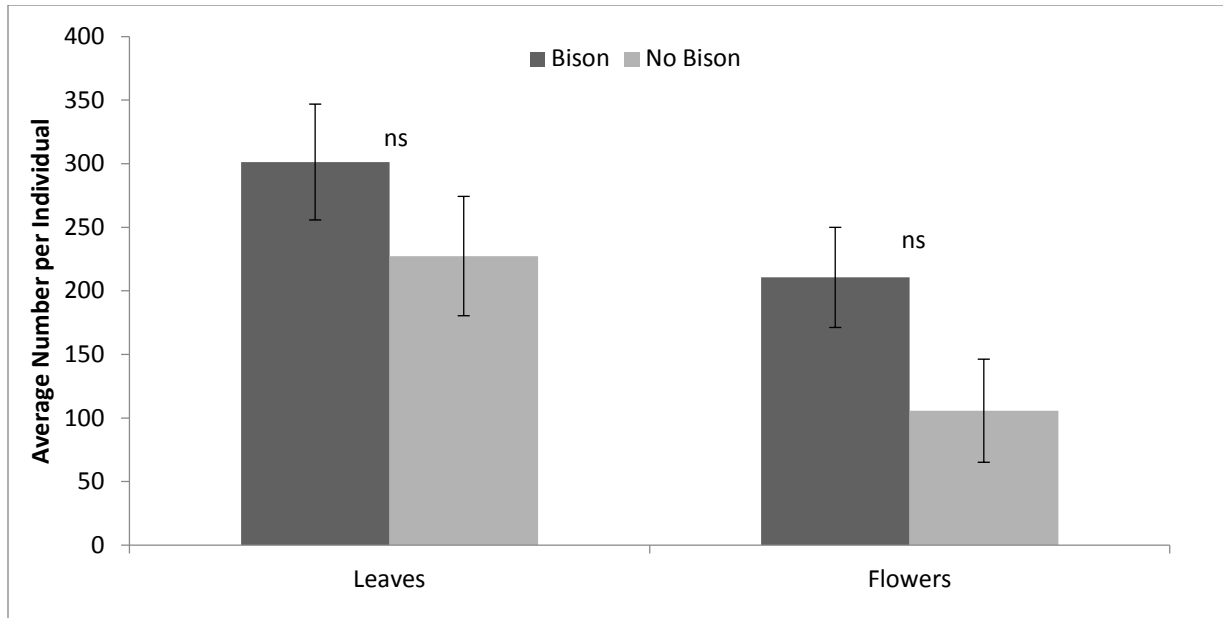**Figure 1.15 *Baptisia australis*: Mean (±SE) number of vegetative and reproductive structures per individual plant in habitats with and without bison.**

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.

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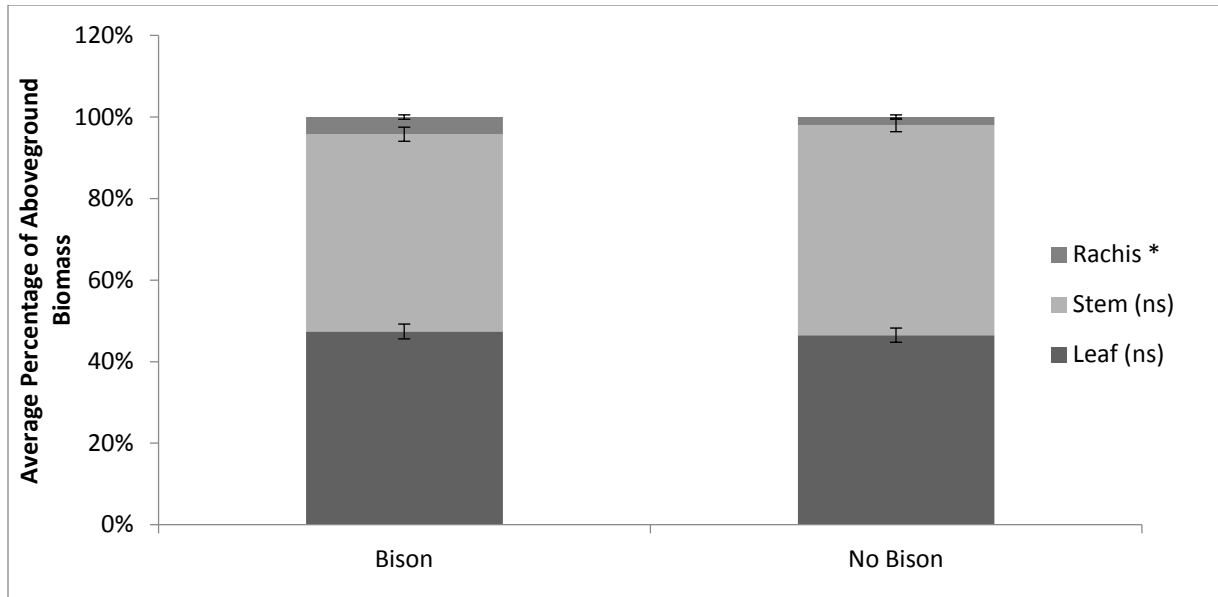
Figure 1.16 *Baptisia australis***: Comparison of biomass allocation patterns (mean ± SE) between individuals grown in bison-present and bison-absent habitats.**

Biomass allocation to each function was calculated as total individual mass of structures devoted to that function divided by total individual biomass. An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.


Figure 1.17 *Baptisia australis*, *Solidago canadensis*, and *Vernonia baldwinii***: Comparison of mean proportional allocation to vegetative reproduction (mean ± SE) between individuals grown in bison-present and bison-absent habitats.**

Proportional allocation to vegetative reproduction was calculated as the ratio of total mass of rhizomes to total aboveground biomass for each individual. An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
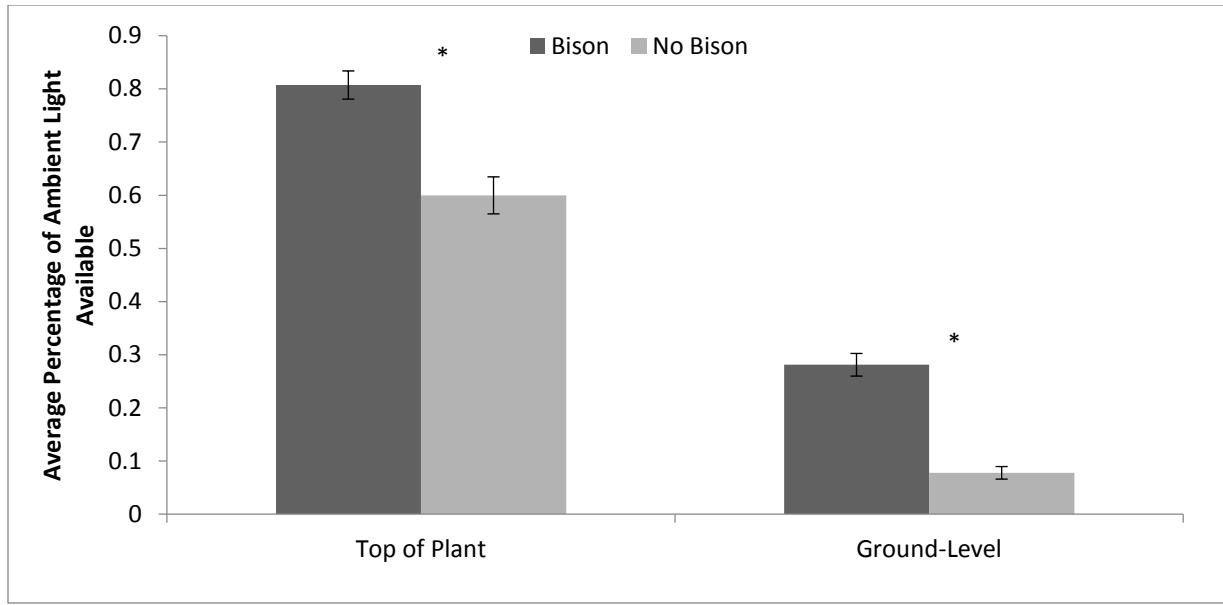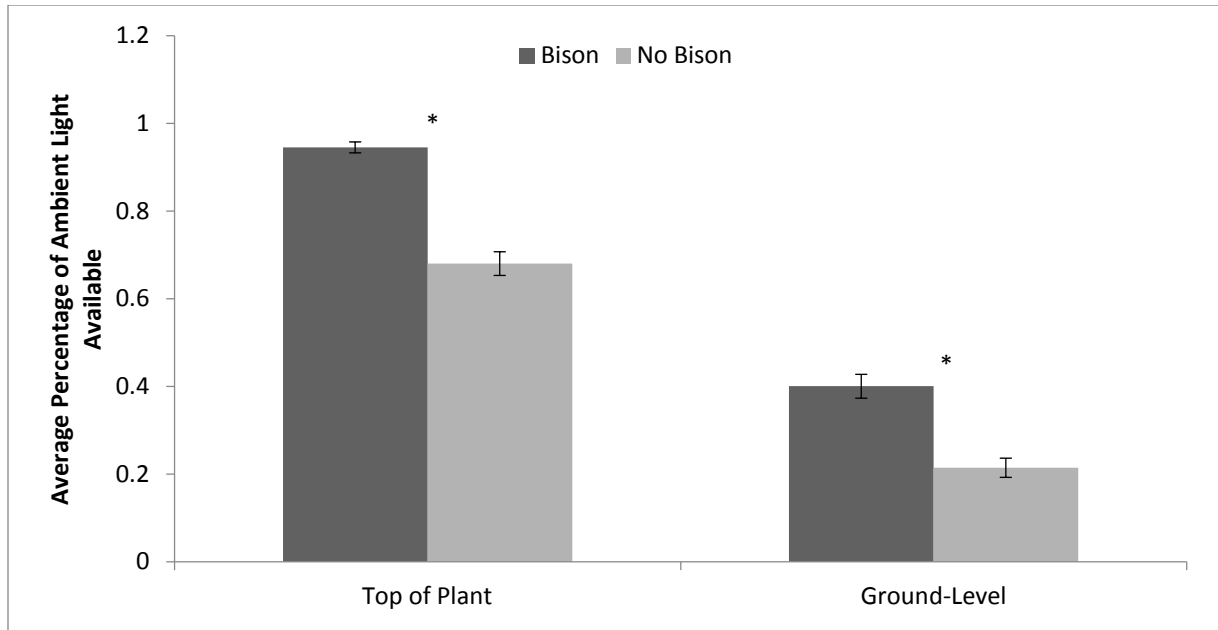
Figure 1.18 *Baptisia australis***: Mean (±SE) percentage of ambient light available at the top of individuals and at soil-level for plants in habitats with and without bison.**

An asterisk represents a significant ($\alpha=0.05$) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
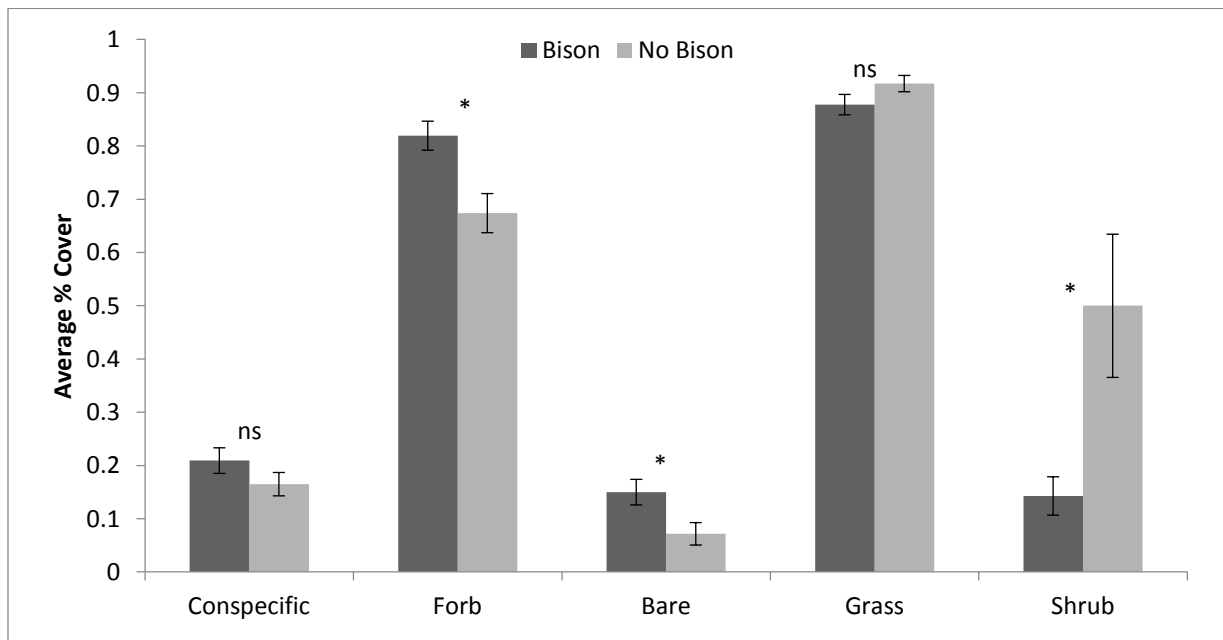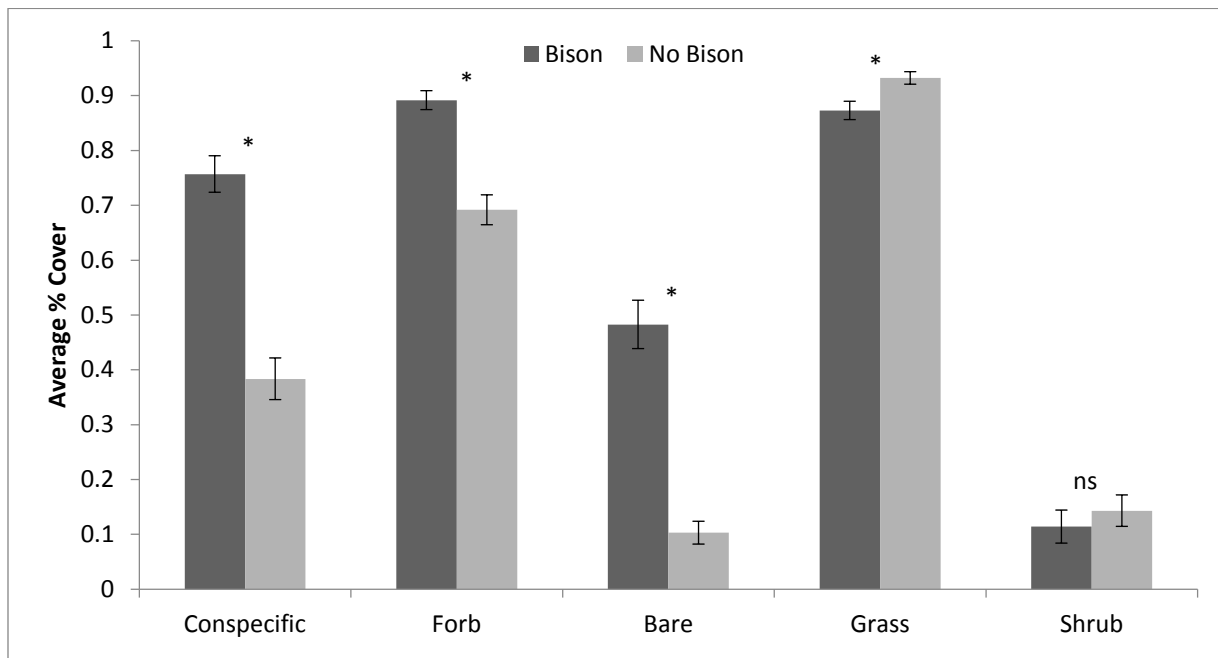

Figure 1.19 *Baptisia australis***: Mean (±SE) percent canopy cover within a 0.5-m^2 sample of vegetation surrounding individuals in habitats with and without bison.**

An asterisk represents a significant ($\alpha=0.05$) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
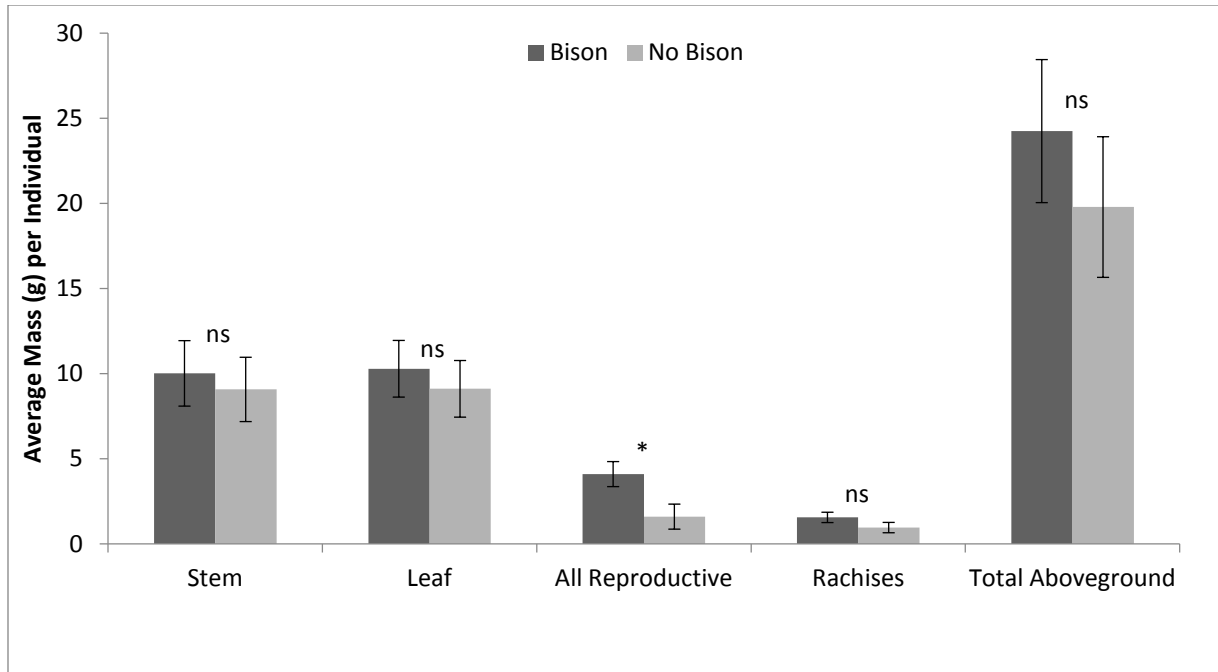
Figure 1.20 *Psoralidium tenuiflorum*: **Mean (±SE) biomass (g) of vegetative and reproductive structures for individuals grown in habitats with or without bison.**

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
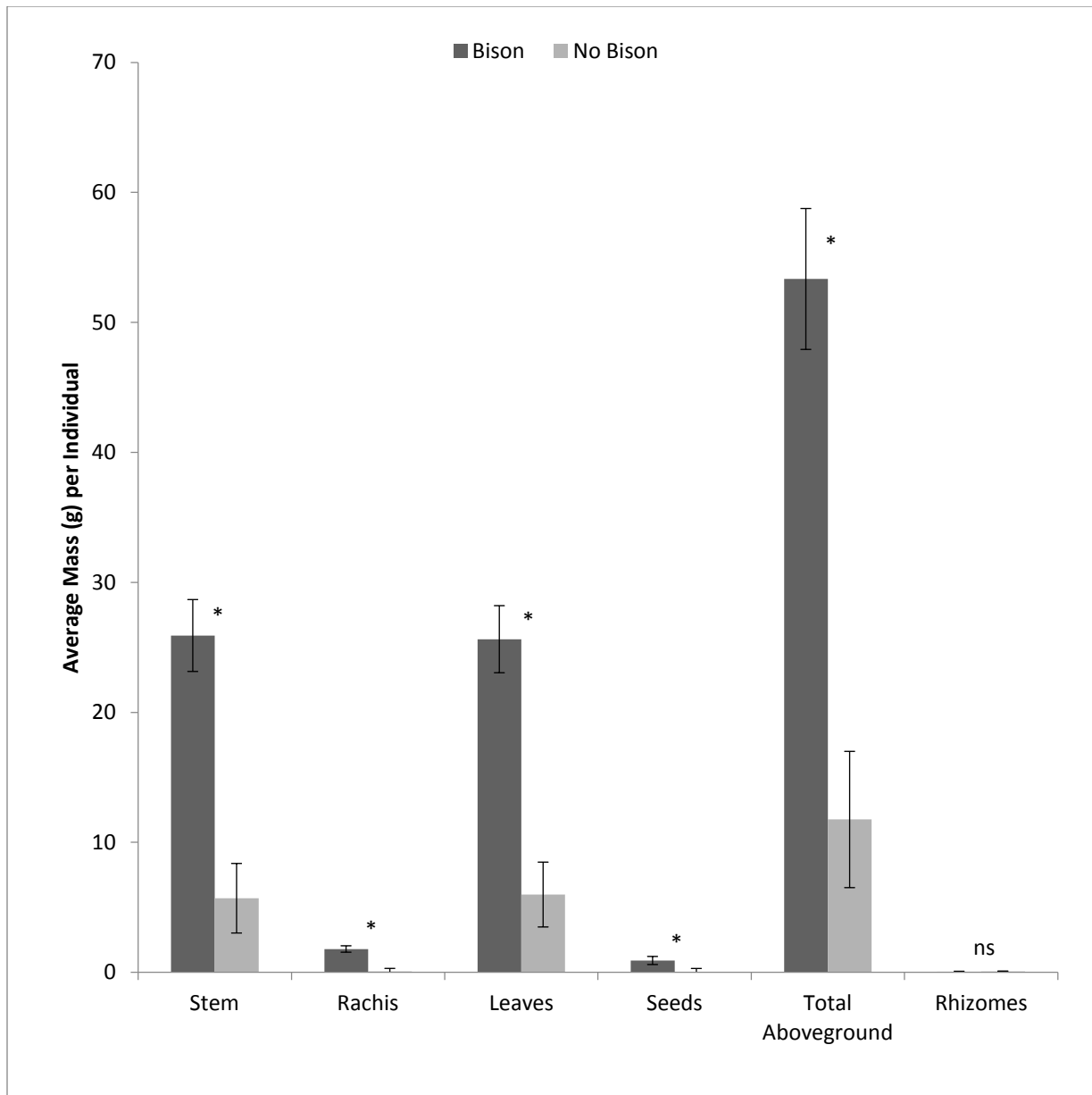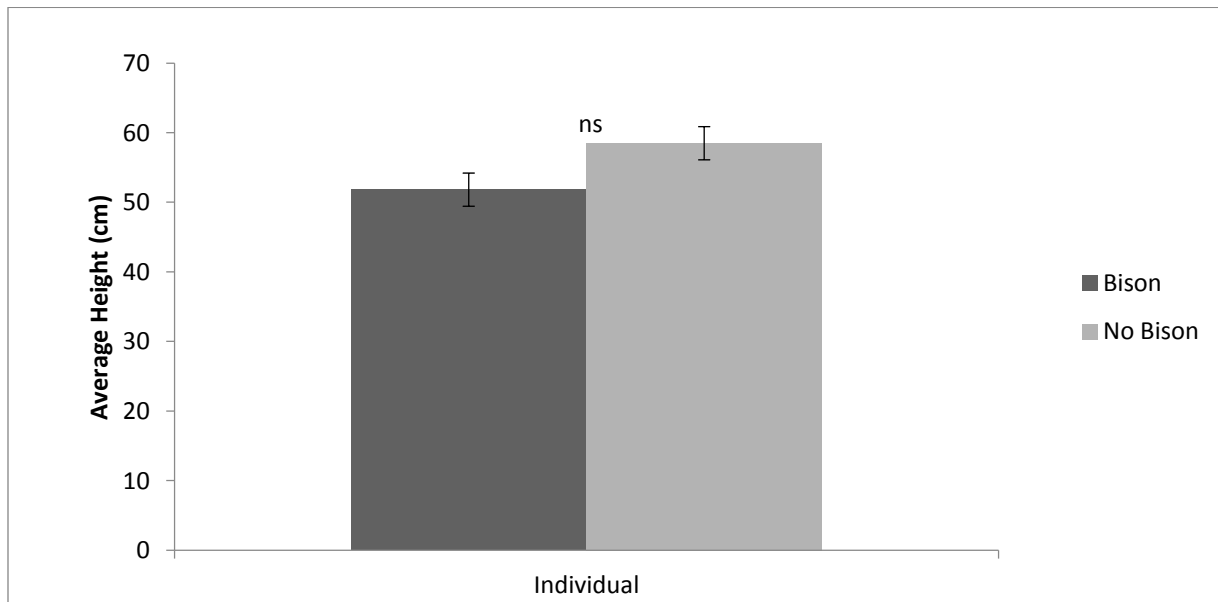

Figure 1.21 *Psoralidium tenuiflorum*: **Mean (±SE) height (cm) of individuals in habitats with and without bison.**

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
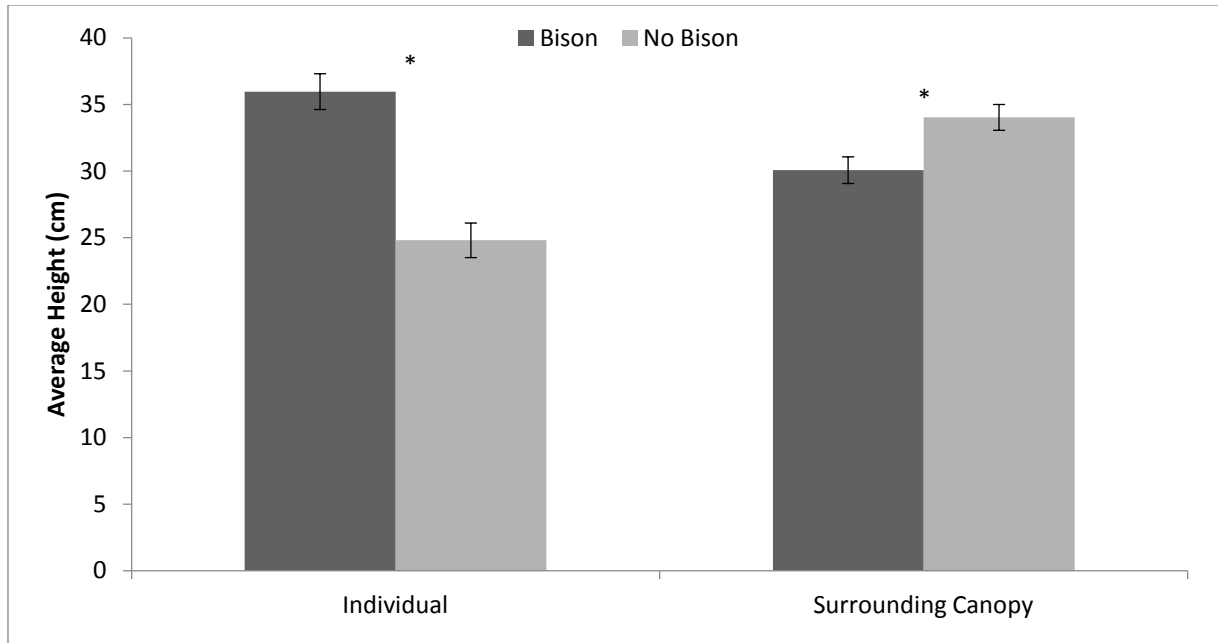
Figure 1.22 *Psoralidium tenuiflorum***: Mean (±SE) number of vegetative and reproductive structures per individual plant in habitats with and without bison.**

An asterisk represents a significant ($\alpha=0.05$) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
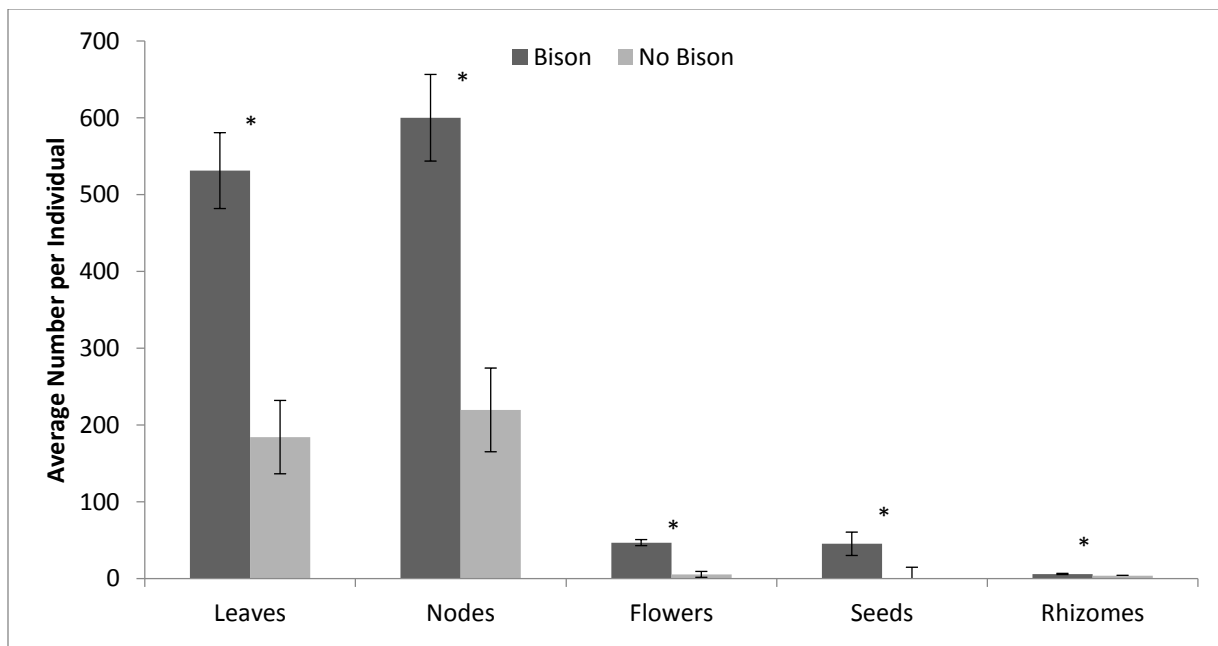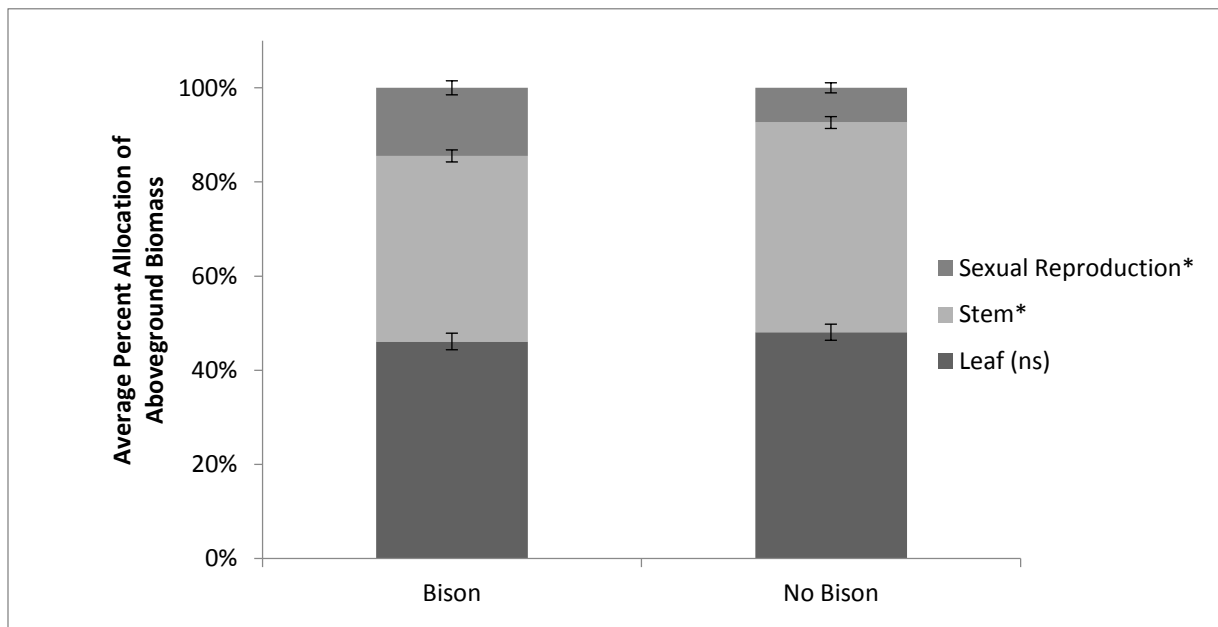

Figure 1.23 *Psoralidium tenuiflorum***: Comparison of biomass allocation patterns (mean ± SE) between individuals grown in bison-present and bison-absent habitats.**

Biomass allocation to each function was calculated as total individual mass of structures devoted to that function divided by total individual biomass. An asterisk represents a significant ($\alpha=0.05$) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
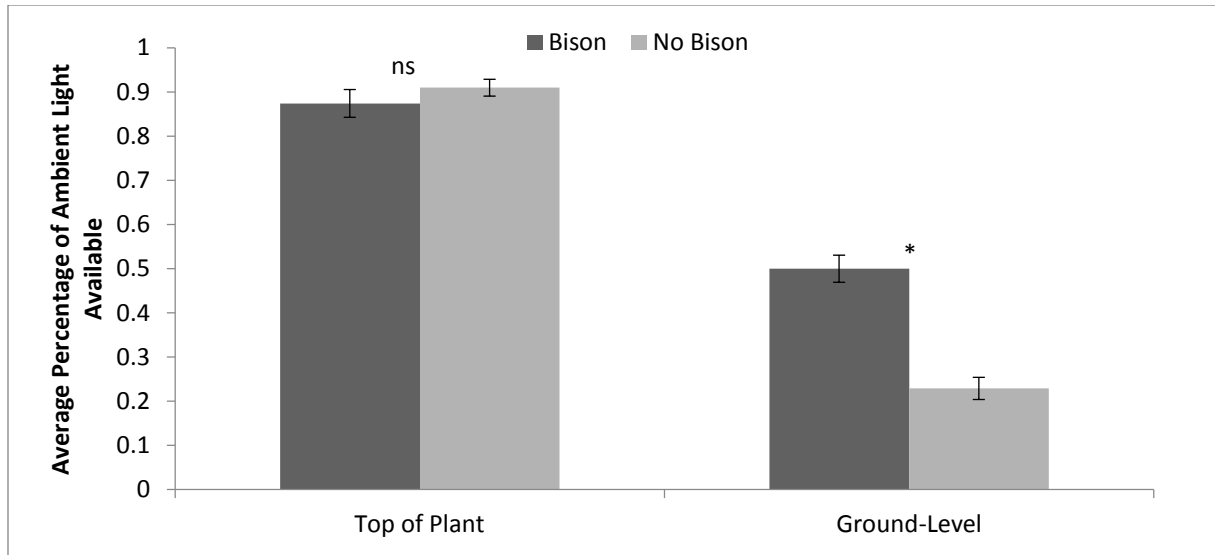
Figure 1.24 *Psoralidium teniflorum*: **Mean (±SE) percentage of ambient light available at the top of individuals and at soil-level for plants in habitats with and without bison.**

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
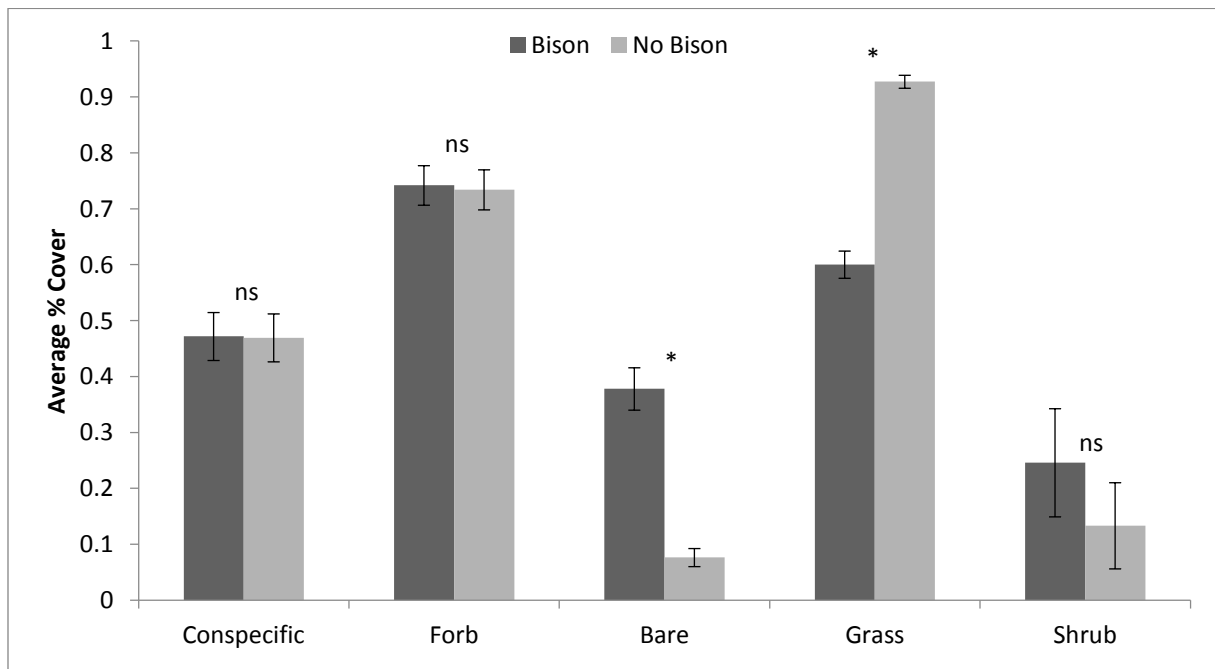
Figure 1.25 *Psoralidium tenuiflorum*: **Mean (±SE) percent canopy cover within a 0.5-m^2 sample of vegetation surrounding individuals in habitats with and without bison.**

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
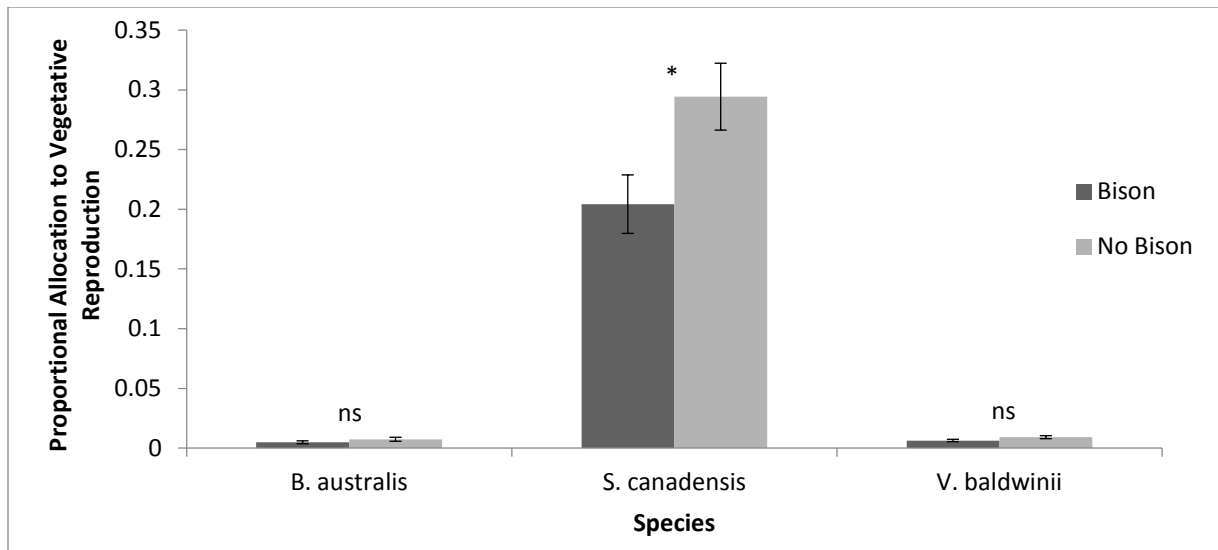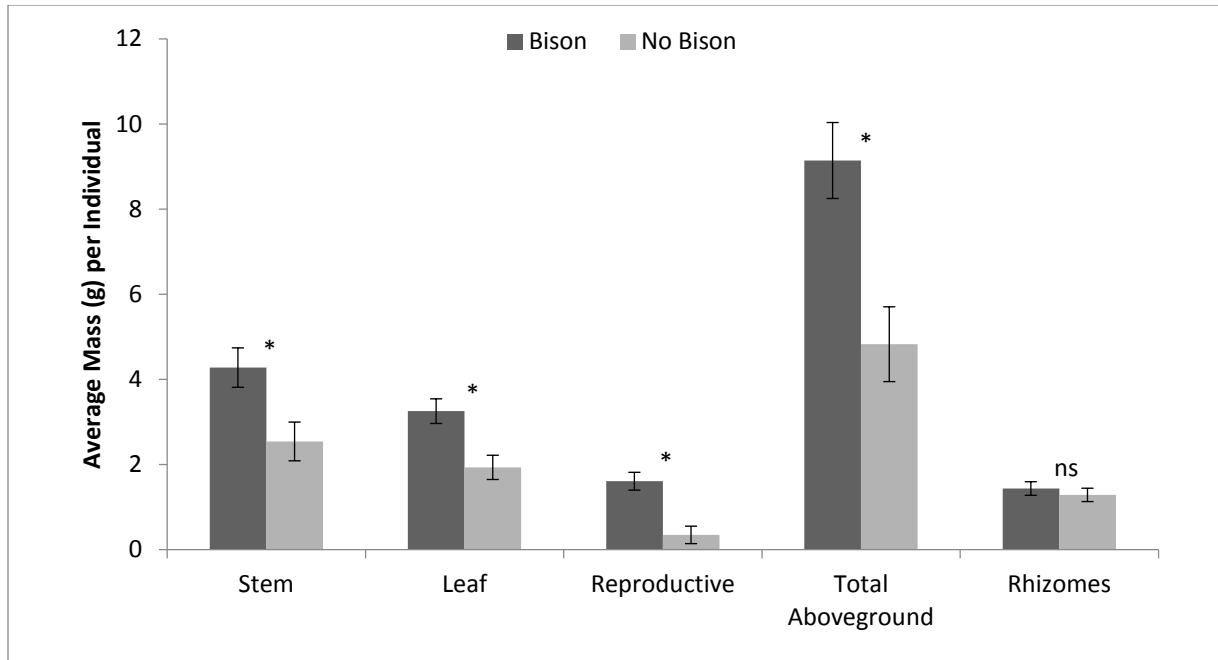
Figure 1.26 *Solidago canadensis*: **Mean (±SE) biomass (g) of vegetative and reproductive structures for individuals grown in habitats with or without bison.**

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
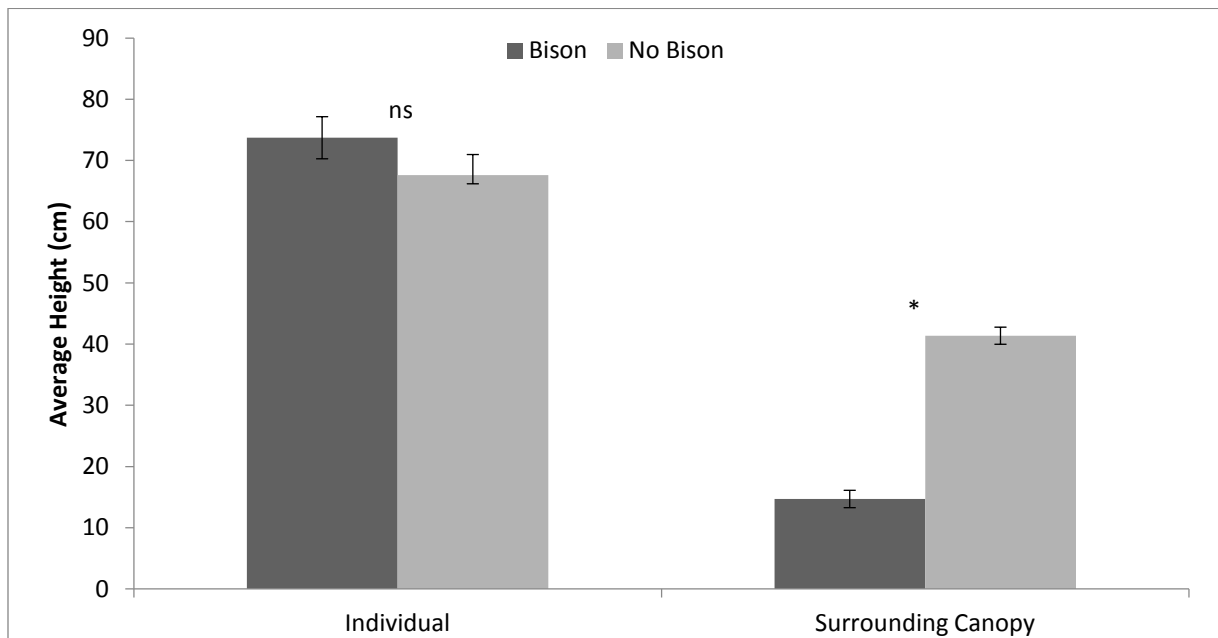

Figure 1.27 *Solidago canadensis*: **Mean (±SE) height (cm) of individuals and the surrounding neighborhood canopy in habitats with and without bison.**

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
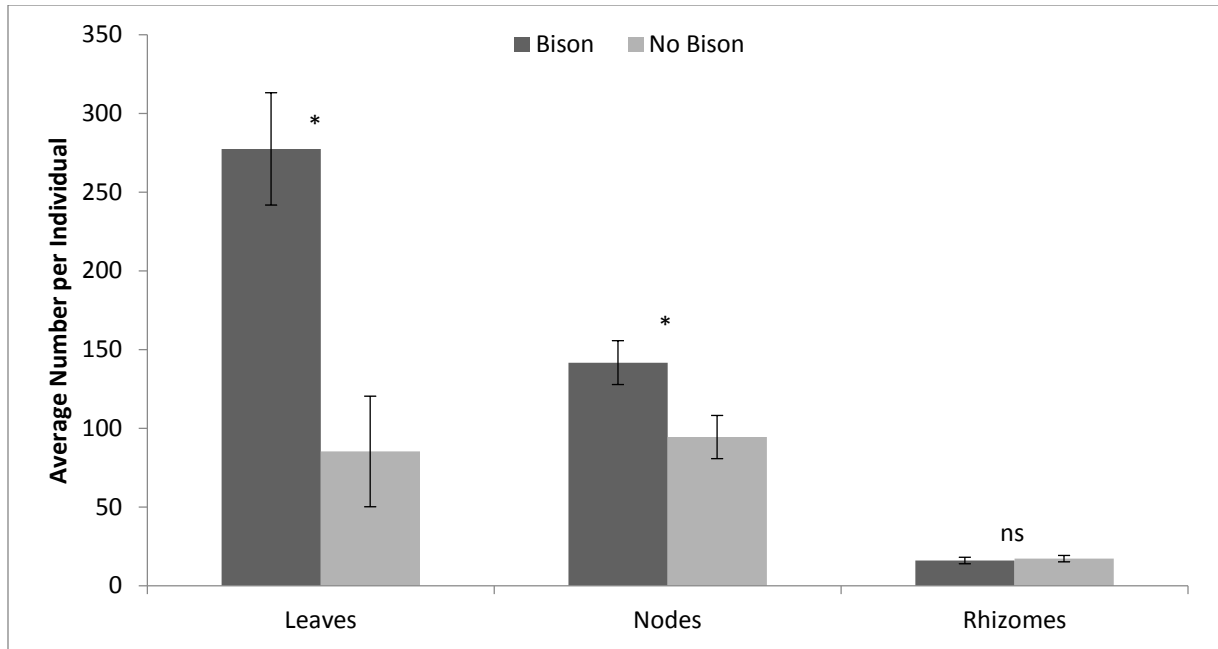
Figure 1.28 *Solidago canadensis*: Mean (±SE) number of vegetative and reproductive structures per individual plant in habitats with and without bison.

Number of nodes here represents number of nodes on main stem, whereas leaf number includes leaves on branches. An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
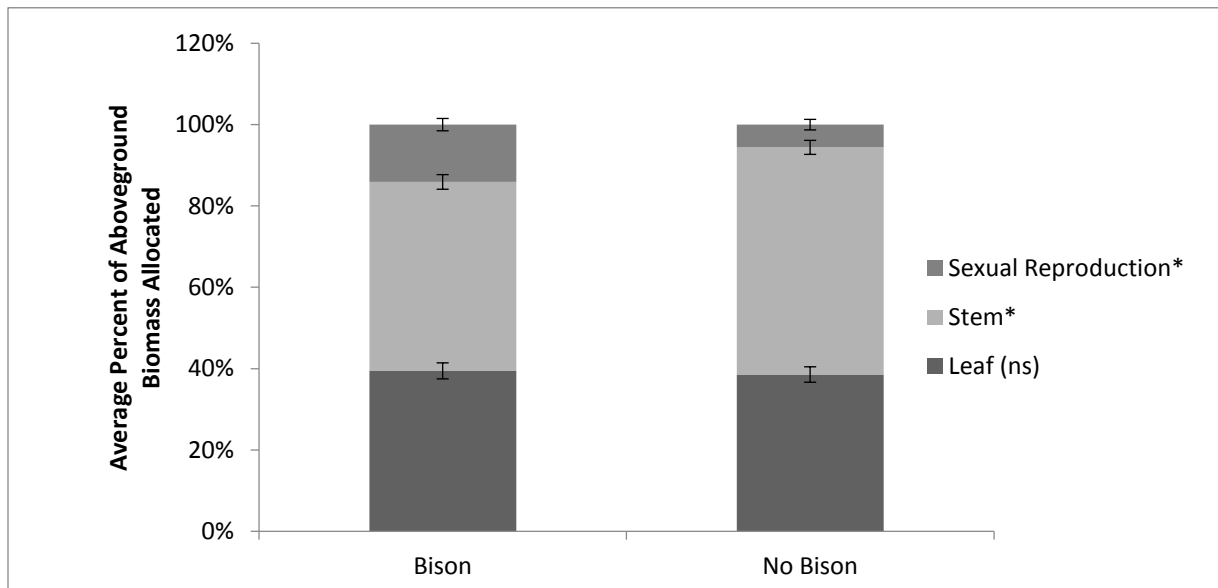

Figure 1.29 *Solidago canadensis*: Comparison of biomass allocation patterns (mean ± SE) between individuals grown in bison-present and bison-absent habitats.

Biomass allocation to each function was calculated as total individual mass of structures devoted to that function divided by total individual biomass. An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
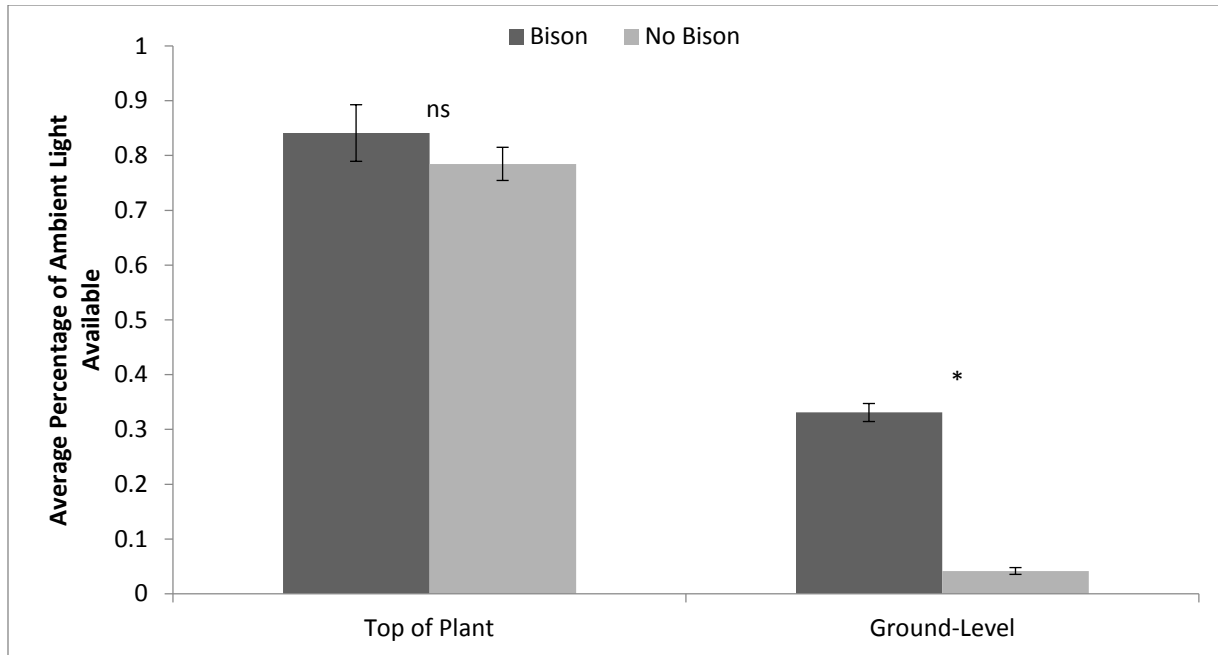
Figure 1.30 *Solidago canadensis*: **Mean (±SE) percentage of ambient light available at the top of individuals and at soil-level for plants in habitats with and without bison.**

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
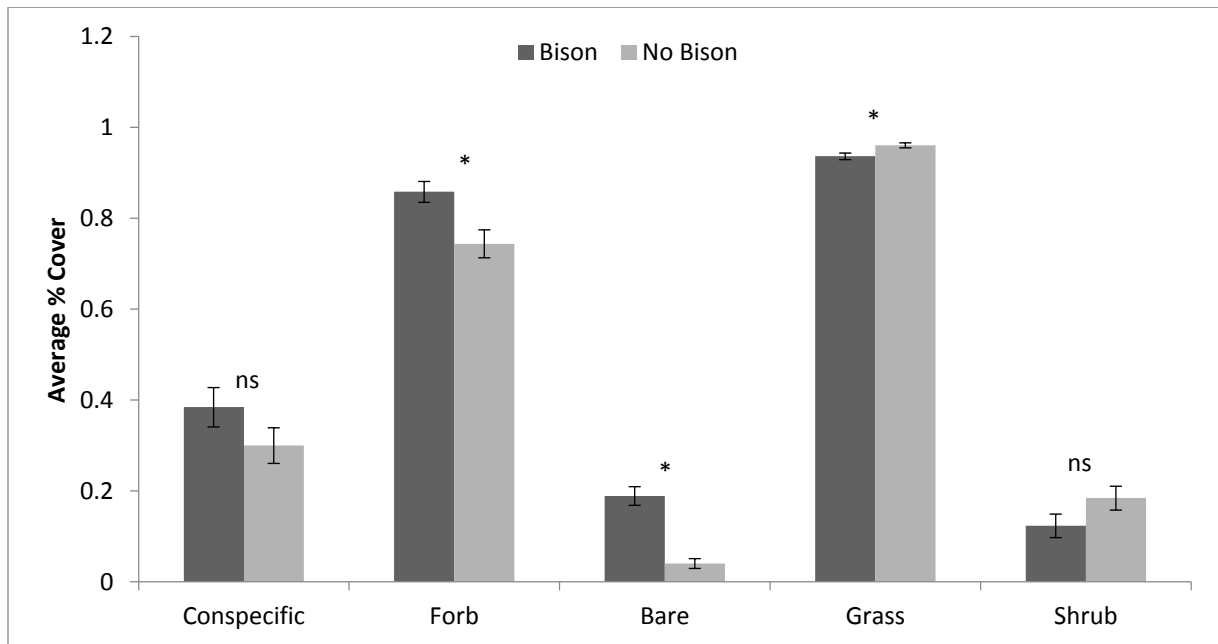

Figure 1.31 *Solidago canadensis*: **Mean (±SE) percent canopy cover within a 0.5-m^2 sample of vegetation surrounding individuals in habitats with and without bison.**

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
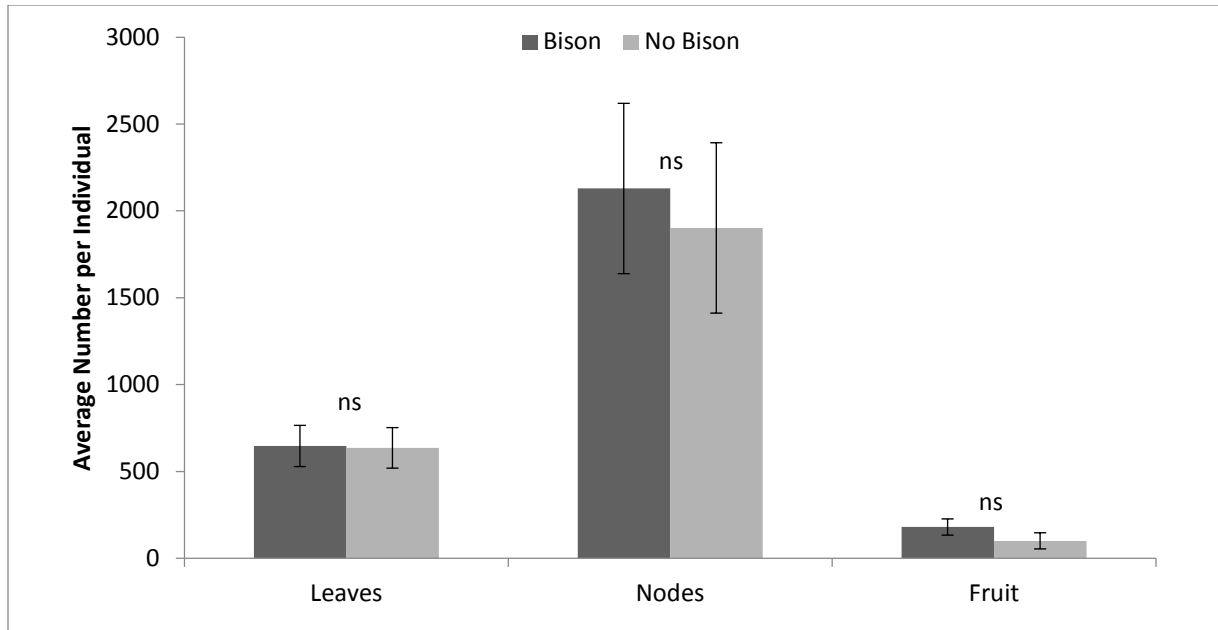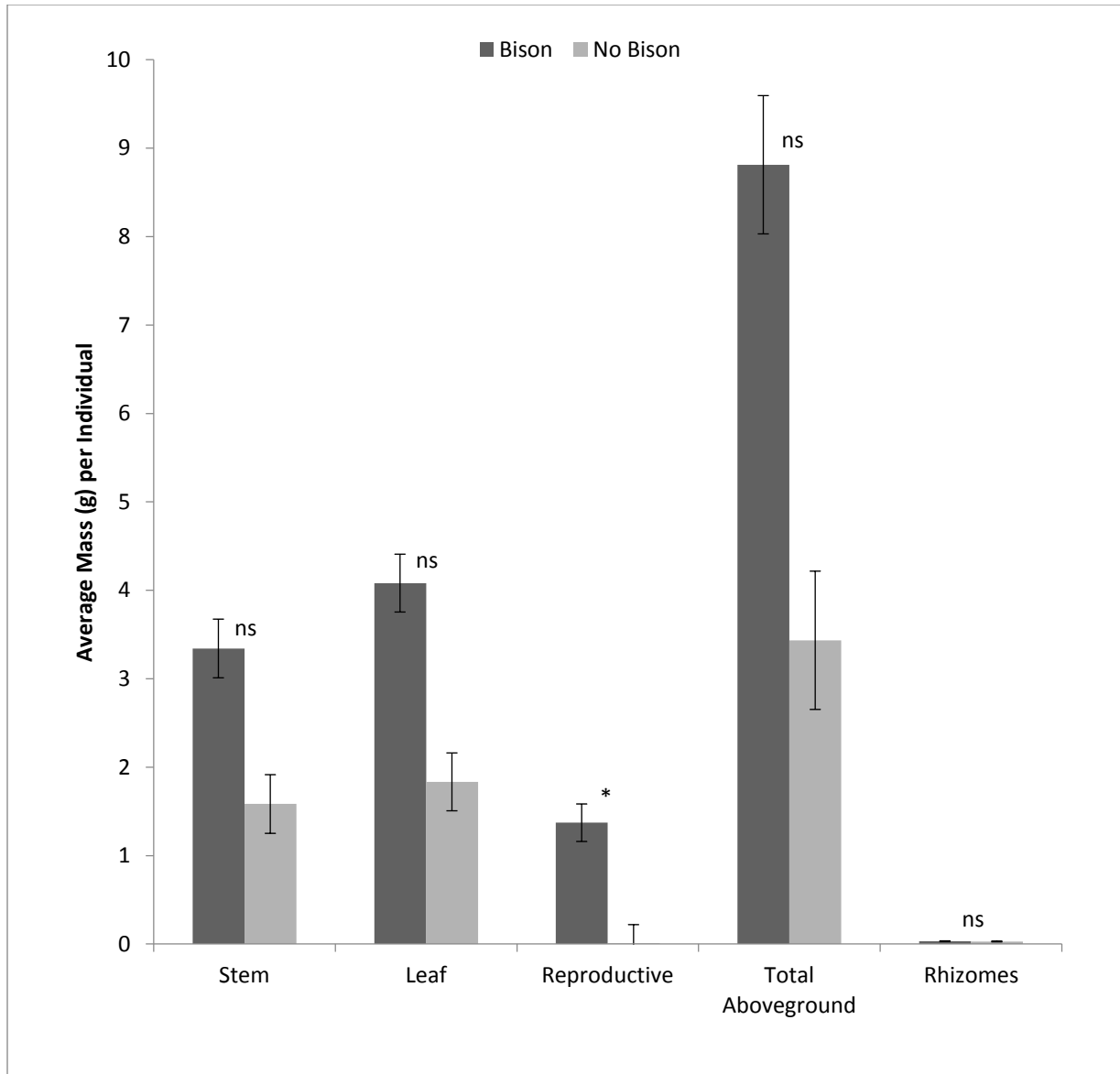
Figure 1.32 *Vernonia baldwinii*: **Mean (±SE) biomass (g) of vegetative and reproductive structures for individuals grown in habitats with or without bison.**

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
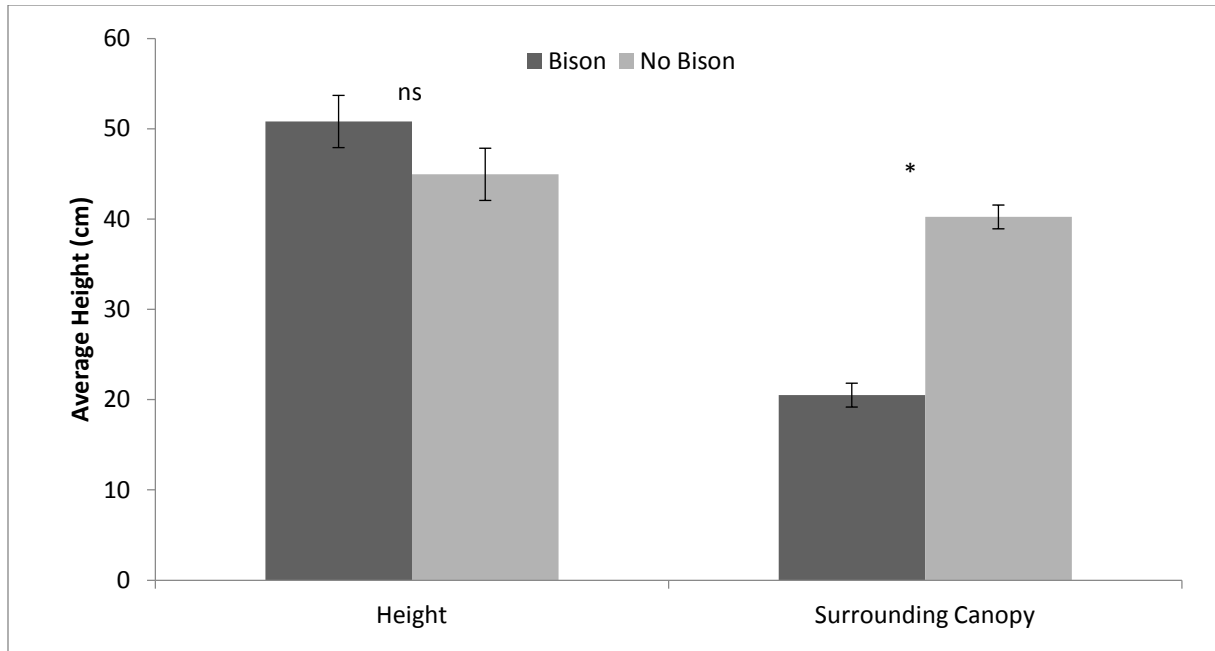
Figure 1.33 *Vernonia baldwinii*: **Mean (±SE) height (cm) of individuals and the surrounding neighborhood canopy in habitats with and without bison.**

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
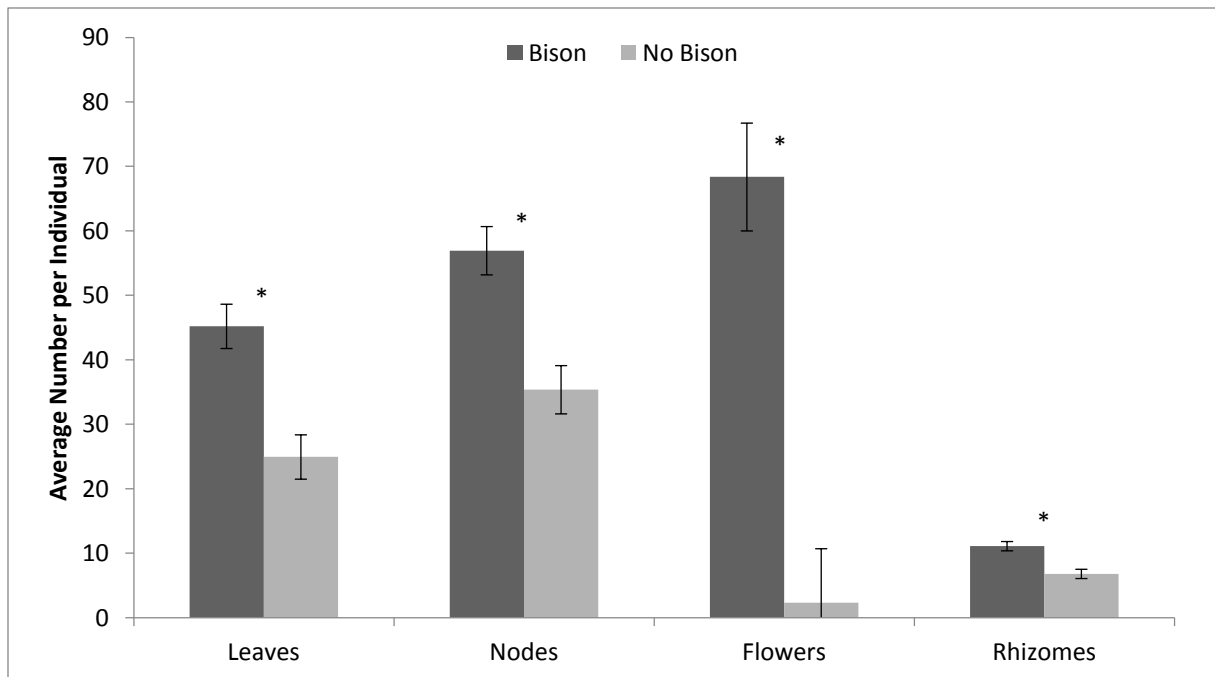

Figure 1.34 *Vernonia baldwinii*: **Mean (±SE) number of vegetative and reproductive structures per individual plant in habitats with and without bison.**

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
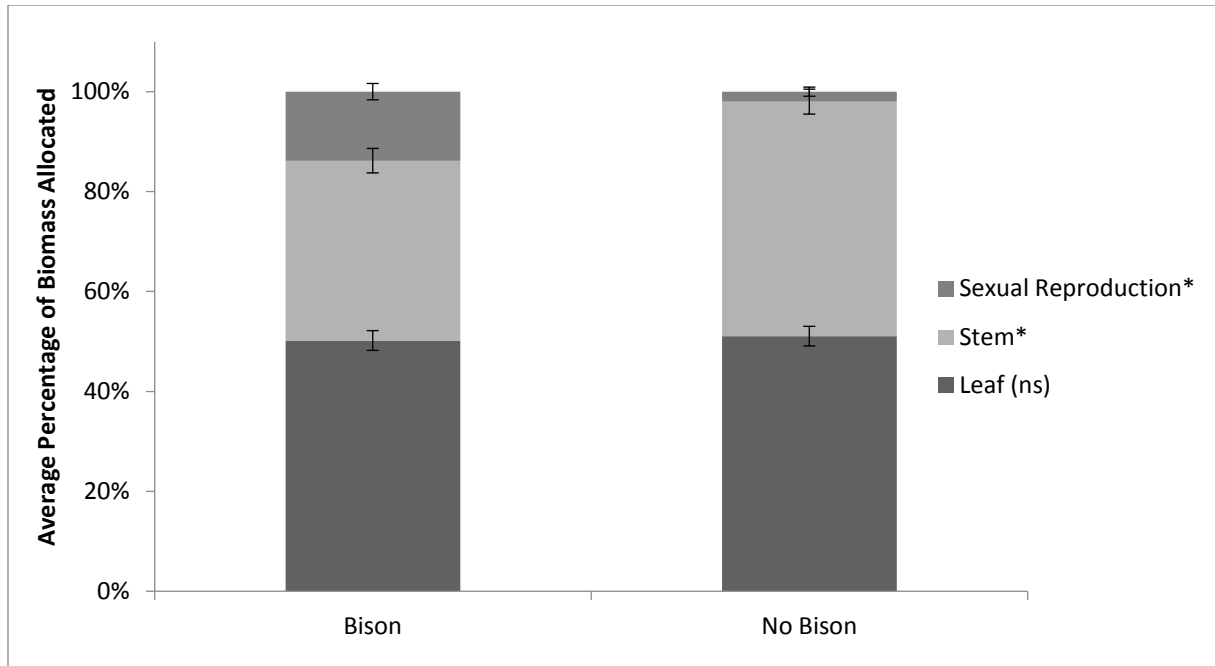
**Figure 1.35 *Vernonia baldwinii*: Comparison of biomass allocation patterns (mean ± SE) between individuals grown in bison-present and bison-absent habitats.**

Biomass allocation to each function was calculated as total individual mass of structures devoted to that function divided by total individual biomass. An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
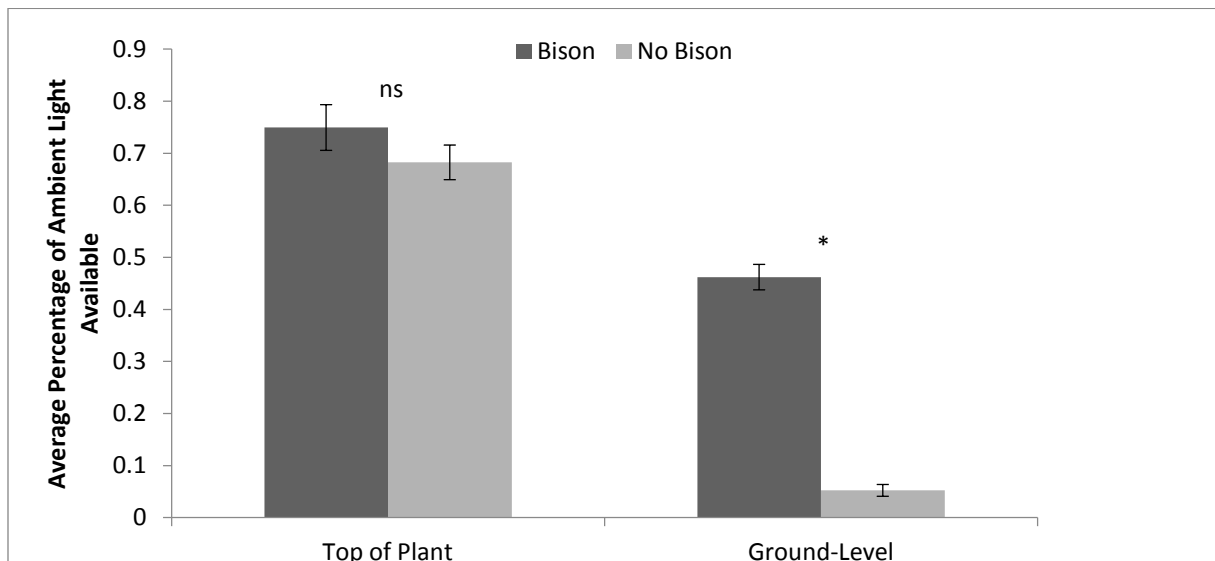

Figure 1.36 *Vernonia baldwinii*: Mean (±SE) percentage of ambient light available at the top of individuals and at soil-level for plants in habitats with and without bison.

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.
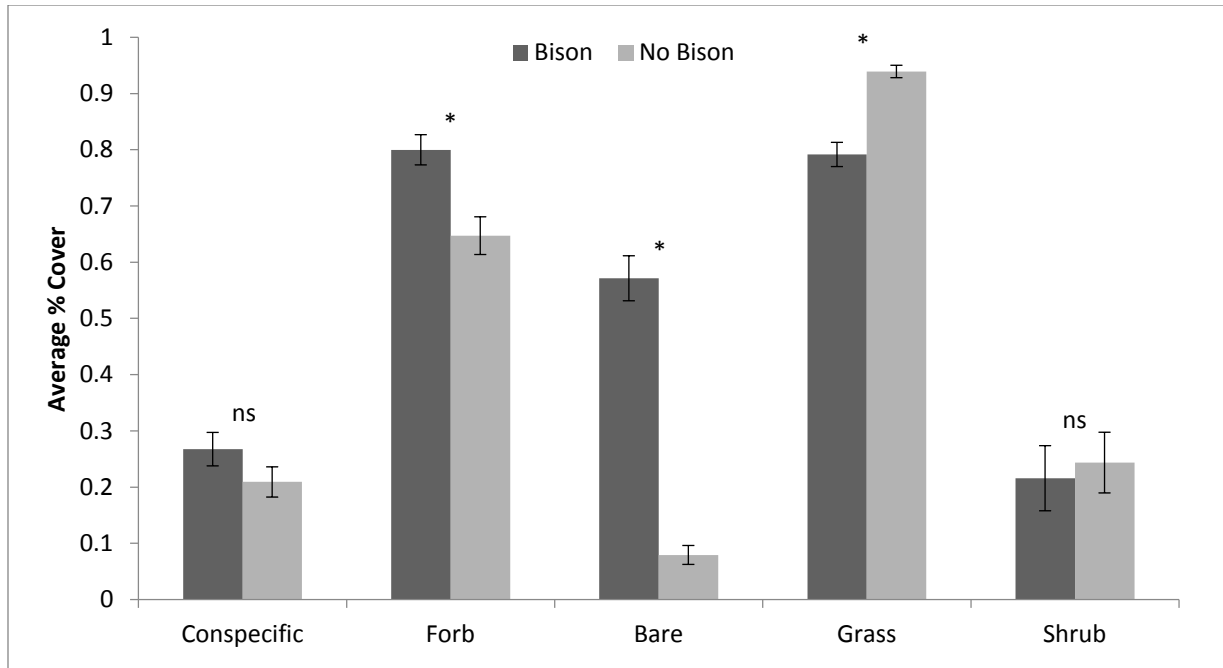
Figure 1.37 *Vernonia baldwinii*: Mean (±SE) percent canopy cover within a 0.5-m^2 sample of vegetation surrounding individuals in habitats with and without bison.

An asterisk represents a significant (α=0.05) difference between bison-present and bison-absent habitats; "ns" indicates that the comparison was not significant.

Chapter 2 - Size-Dependency of Differences in Forb Reproduction between Grazed and Ungrazed Tallgrass Prairie

Abstract

This study sought to determine whether differences in reproduction between bison-grazed and ungrazed tallgrass prairie habitats are size-dependent for six species of perennial forb, and whether there is a trade-off between allocation to sexual and vegetative reproduction for two of those species. The species studied were *Ambrosia psilostachya*, *Artemisia ludoviciana*, *Baptisia australis*, *Psoralidium tenuiflorum*, *Solidago canadensis*, and *Vernonia baldwinii*. Sexual reproduction was measured for six species as number of fruits/flowers, sexual reproductive effort (SRE), and total mass of reproductive structures. Vegetative reproduction was measured for three species as number of rhizome buds, vegetative reproductive effort (VRE), and total mass of rhizome buds. Plant size was determined using total aboveground biomass. Sexual reproduction was generally positively correlated with size, and some relationships differed between habitats for five of the six species studied. Rhizome number was weakly, positively correlated with size for two out of three species, but other measures of vegetative reproduction did not clearly vary proportionately with size. There was no evidence of a trade-off between sexual and vegetative reproduction for the two species studied. The results of this study provide evidence that differences in reproduction between bison-grazed and ungrazed habitats are not entirely size-dependent and that vegetative reproduction may be regulated differently than sexual reproduction.

Introduction

Reproduction is a key component of plant life history and fitness, so improving our understanding of how plants alter reproduction in response to environmental changes is an important question in plant ecology. Shifts in plant reproduction can, over time, lead to changes in population dynamics, so this issue is of particular importance in ecosystems of conservation concern like the highly endangered tallgrass prairie of central North America. This study will investigate whether previously-ascertained differences in reproduction between two management regimes are size-dependent for six species of native perennial forb. Five of the six species showed significantly greater reproduction in habitats with bison present than in ungrazed habitats, and four of the six were significantly larger on average; no species were smaller or decreased reproduction in bison-present habitats (Chapter 1).

Allocation to sexual reproduction, like other aspects of plant life history, has the potential to be influenced by a multitude of factors, both extrinsic and intrinsic (Karlsson & Mendez 2005). Disturbance and density of neighbors (Harper 1977; Holler & Abrahamson) and limitation of resources such as light and nutrients (Chabot 1978; Shefferson et al. 2006) can affect allocation to sexual reproduction. Particularly for long-lived perennials, allocation to sexual reproduction can be constrained by the need to also allocate resources to other functions such as survival and defense and by physiological or structural limitations (Bazzaz et al. 1987; Karlsson & Mendez 2005). For many species, sexual reproduction has been shown to increase with plant size, perhaps since larger plants have more photosynthetic area and thus more resources to devote to reproduction (Aarssen & Taylor 1992; Cheplick 2005; Hartnett 1990; Hautier et al. 2009; Weiner et al. 2009). Many species seem to have a size threshold for sexual reproduction below which individuals will fail to reproduce (Schmid et al. 1995). Plant growth is often allometric, i.e. different organs grow at different rates, so shifts in proportional allocation

to certain organs may be due to changes in plant size rather than to adaptive phenotypic changes in response to different environments. Since disturbance, herbivory, and density of neighbors can all affect resource availability, which can in turn influence size, it can be difficult sometimes to determine whether shifts in sexual reproductive allocation between habitat types are due to a true response to habitat differences or simply to greater resource availability enabling plants to increase their size and, consequently, their sexual reproductive allocation (Cheplick 1995).

Vegetative reproduction, or the creation of new individuals from belowground rhizome buds, has not been studied as widely as sexual reproduction. However, there is some indication that it too can be influenced by resource availability (Chabot 1978; Liu et al. 2009; Steufer & Huber 1998; Xie et al. 2014), disturbance, herbivory (Benot et al. 2013), neighbor density (Holler & Abrahamson 1977; Underwood & Halpern 2012), and plant size (Schmid et al. 1995; Underwood & Halpern 2012; Xie et al. 2014). Since they both require investment of the plant's resources but do not primarily function to aid in resource acquisition and are thus "costly" to an individual, it has been argued by many that there should be a trade-off between vegetative and sexual reproduction wherein an increase in allocation to one form of reproduction should be accompanied by a proportional decrease in allocation to the other (Hartemink et al. 2004; Novakova et al. 2012; Thompson & Eckert 2004). Which mode of reproduction the plant favors would depend upon the environmental pressures acting on an individual. However, some studies have failed to find support for the notion of a trade-off between the two forms of reproduction (Mendoza & Franco 1998; Schulze et al. 2001).

Large ungulate grazers such as bison can tremendously impact prairie plant community structure by selectively consuming certain species and thus altering competitive relationships among species and, hence, plant growth and allocation. Bison have been shown to alter nutrient

availability, increase light availaibility, decrease vegetation density, and to generally increase

disturbance level and environmental heterogeneity (Chapter 1; England & DeVos 1969; Hartnett

et al. 1996; Knapp et al. 1999; Steinhauer and Collins 1995). Any of these habitat changes could

potentially alter allocation to reproduction, plant size, and the relative importance of vegetative

and sexual reproduction for clonal species.

This study examined three questions about reproductive allocation in six species of

perennial forbs in tallgrass prairie: 1) Are differences in sexual reproduction between bison-

present and bison-absent habitats merely size-dependent? If differences in sexual reproduction

between habitats with and without bison are primarily due to differences in mean plant size

between habitats, then size will be a strong predictor of sexual reproduction and the relationship

between size and reproduction will not vary between plants grown in bison-grazed and ungrazed

habitats. 2) Is allocation to vegetative reproduction related to size, and is the relationship

different between individuals grown in bison-present and bison-absent habitats? If allocation to

vegetative reproduction is size-dependent, then size will be a strong predictor of vegetative

reproduction. 3) Is there a trade-off between allocation to vegetative and sexual reproduction,

and does the relationship between the two differ between bison-present and bison-absent

habitats? If there is a trade-off between allocation to vegetative and sexual reproduction, then

there will be a significant negative correlation between the two variables. Alternatively, if both

forms of reproduction increase with size, there will be a positive correlation between measures of

vegetative and sexual reproduction. For all three questions, the presence of bison in the habitat

will be considered to have size-independent effects on reproduction if any of the relationships

between reproductive allocation and plant size studied differ significantly between populations in

habitats with and without bison. By determining whether allocation to sexual and vegetative

reproduction are related to one another or to size, and whether those relationships differ between

two very different habitats, I hope to add to our understanding of how plant size and

environmental factors influence plant reproductive allocation.

Methods

Site Description

This study was conducted at Konza Prairie Biological Station (KPBS), a 3487-hectare tallgrass prairie preserve which is jointly owned and run by the Nature Conservancy and Kansas State University. One of the six original NSF Long-Term Ecological Research Sites, KPBS is located in the Flint Hills ecoregion of Kansas (39°05′N, 96°35′W). The region is characterized by a continental climate with average monthly temperatures ranging from -2.7 to 26.6ºC. Average annual precipitation at KPBS is 835mm, approximately 75% of which falls during the growing season (Bark 1987). Between April 1 and October 31 of 2013, the year of this study, approximately 672mm of precipitation fell and temperatures ranged from -4.3 to 39.7ºC with an average of 19.4ºC (LTER dataset AWE012). KPBS is subdivided by watershed into numerous fire (burned every 1, 2, 4, or 20 years since 1972) and grazing management regimes (ungrazed, grazed by bison, grazed by cattle). Bison have been present in the native grazer treatments since 1987, allowing for the study of the long-term impacts of bison on plant communities (Knapp et al 1998). The vegetation of KPBS consists primarily of unplowed tallgrass prairie dominated by warm-season perennial grasses such as big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* Michx.), and Indiangrass (*Sorghastrum nutans* L.). Subdominant vegetation includes a diverse mix of forbs, cool-season grasses, and a few woody species. Over 576 species of vascular plant have been identified at KPBS from over 96 families, but over 40% of species belong to the families Poaceae, Asteraceae, Fabaceae, and Cyperaceae alone (Towne 2002). This study, conducted in 2013, sought to compare the growth and reproduction of plants in communities where bison were present with similar communities that lack bison. In this study, samples were taken from a total of three watersheds, all of which were

burned at 2-year intervals, most recently in spring 2012: N2A (bison-present treatment) and 2A and 2B (bison-absent treatment).

Species Description

Over 576 species of vascular plant have been identified in KPBS, of which over 75% are forbs (Towne 2002). From these, a total of six common, native, perennial forb species were chosen for this study as representatives of two of the most species-rich forb families found in tallgrass prairie: Asteraceae and Fabaceae. None of the species chosen for this study are considered palatable to large ungulate grazers. *Ambrosia psilostachya* DC., *Artemisia ludoviciana* Nutt., *Vernonia baldwinii* Torr., *and Solidago canadensis* L. are all rhizomatous representatives of Asteraceae. The rhizomatous *Baptisia australis* (L.) R. Br. and non-rhizomatous *Psoralidium tenuiflorum* (Pursh) Rydb. are both members of Fabaceae and are typically found in rocky upland or hillside prairies. They bloom April-June and are primarily insect-pollinated. *Ambrosia psilostachya* and *Artemisia ludoviciana* are both widespread in open prairies and primarily wind-pollinated, blooming August-October.   *Solidago canadensis* is most common in lowland sites, is primarily insect-pollinated, and blooms August-October. *Vernonia baldwinii*, also primarily insect-pollinated, is widespread in open prairies and blooms July-September.

Field Sampling

For each species, six naturally-occurring populations on similar terrain were located for sampling, three in the bison-present treatment and three in the bison-absent treatment. Within each population, a randomly-placed transect was used to select twelve individuals at randomly-chosen intervals of at least 2m. Thus, a total of 72 individuals of each species were randomly chosen for use in this study (36 in bison-present habitats and 36 in bison-absent habitats). The

placement of a transect for any one species did not affect the placement of transects for any other species. All individuals in the bison-present treatment were located in watershed N2A, but the plants sampled in the bison-absent treatment were split between the watersheds 2A and 2B at KPBS. Each individual was marked with a flag and metal tag in early May and followed throughout the growing season until it reached peak flower. An individual was defined as a single ramet for *A. psilostachya*, *A. ludoviciana*, *S. canadensis*, and *V. baldwinii*. For *B. australis* and *P. tenuiflorum*, an individual was defined as the marked stem and all living connected stems. If a marked individual died (or senesced prematurely), the nearest conspecific was chosen as a replacement and the death was noted. No signs of bison herbivory were observed on any individuals marked for use in this study.

Individuals were harvested when they reached peak flower or, in the case of vegetative individuals, when all neighboring individuals were at peak flower and no signs of reproductive development were discernible. The determination of when a reproductive individual was considered to be in peak flower varied according to species. For the anemochorous species *A. ludoviciana*, *S. canadensis*, and *V. baldwini*, individuals were considered at peak flower when all (or nearly all) flowers had reached full size but before the earliest-developing flowers released any propagules to the wind. *Ambrosia psilostachya* was considered at peak flower when all male and female flowers had reached full size. Since the fruits of *B. australis* and *P. tenuiflorum* are much heavier than the flowers, those species were considered to be in peak flower when all (or nearly all) flowers had developed into mature fruit. Whether each harvested individual was reproductive or vegetative was recorded. Since it is nonclonal, *P. tenuiflorum* was harvested by clipping stems at soil level, but all other species were excavated in order to collect underground vegetative reproductive structures. Extracting all root biomass was impractical in Konza's

rocky, clay-rich soil, but every effort was made to remove all rhizomes associated with each chosen individual. Ultimately, 29-36 individuals per treatment were harvested for each species (Table 2.1).

Biomass Allocation

After harvest, the aboveground portions of each plant were dissected into three main functional components: growth/support (stems), photosynthesis (leaves), and sexual reproductive structures (including flowers, bracts, and some peduncles/rachises). Only live tissues were retained for analysis. All parts of the plant were then oven-dried at 60º C for at least 72 hours, then weighed to the nearest 0.001g using a Mettler AE 100 scale immediately upon removal from the drying oven. Since herbivorous insects consumed a substantial quantity of the flowers and developing fruits of *B. australis*, making it impossible to determine the true weight of reproductive material produced, the mass of floral stems (rachis/peduncle) was used as an approximation of reproductive biomass for all individuals of this species. The number of flowers or fruits (or floral nodes in the case of *B. australis*) produced by each individual was also determined during dissection as an estimate of potential fecundity for each species except *S. canadensis*. Herbivorous insects also consumed many flowers of *P. tenuiflorum*, and only non-damaged fruits and flowers were counted for this species since that represents a more accurate estimate of functional fecundity than a count that included unviable flowers or fruit, and any potential bison-mediated differences in insect herbivory would be relevant to the survival and success of plant species. For each individual, all parts for each functional component were weighed together. Sexual Reproductive Effort (SRE) was calculated as the ratio of total mass of sexual reproductive structures to total mass of aboveground vegetative structures (leaves and stems) for each individual.

Of the five rhizomatous species studied, only three species had rhizomes that were sufficiently developed by time of harvest for analysis: *B. australis*, *S. canadensis*, and *V. baldwinii*. For each species, all developing rhizomes associated with each harvested individual were counted, excised, and collected. The rhizomes for each individual were then oven-dried at 60º C for at least 72 hours, then collectively weighed to the nearest 0.001g using a Mettler AE 100 scale immediately upon removal from the drying oven to attain the total mass of rhizomes per individual. Vegetative Reproductive Effort (VRE) was calculated as the ratio of total mass of rhizomes to total mass of aboveground vegetative structures (leaves and stems) for each individual.

Analysis

Relationships between allocation to sexual reproduction and size were examined for all six species and compared between individuals grown in habitats with and without bison. For each species, separate regression analyses were used to determine whether there was a significant relationship between 1) number of flowers/fruits and total aboveground biomass, 2) SRE and total aboveground biomass, and 3) (to show the relative contribution of shifts in mass of vegetative and reproductive parts to variation in SRE) total mass of sexual reproductive organs and vegetative structures for individuals grown in habitats with and without bison. ANCOVA was used to determine whether grazing significantly altered any of those three relationships by determining whether grazing or the interaction between the y-variable and grazing contributed significantly to the model (Cheplick 2005).

Relationships between allocation to vegetative reproduction and size were examined for *B. australis*, *S. canadensis*, and *V. baldwinii* and compared between individuals grown in habitats with and without bison. For each species, separate regression analyses were used to determine

whether there was a significant relationship between 1) number of rhizomes and total aboveground biomass, 2) VRE and total aboveground biomass, and 3) (to show the relative contribution of shifts in mass of rhizomes and aboveground vegetative structures to variation in VRE) total mass of rhizomes and aboveground vegetative structures for individuals grown in habitats with and without bison. ANCOVA was used to determine whether grazing significantly altered any of those three relationships by determining whether grazing or the interaction between the y-variable and grazing contributed significantly to the model.

The possibility of a trade-off between allocation to sexual and vegetative reproduction was also examined for *S. canadensis*, and *V. baldwinii* and compared between individuals grown in habitats with and without bison. For each species, separate regression analyses were used to determine whether there was a significant relationship between 1) VRE and SRE and 2) total mass of rhizomes and of sexual reproductive organs for individuals grown in habitats with and without bison. ANCOVA was used to determine whether grazing significantly altered any of those relationships.

Results

Ambrosia psilostachya

Sexual reproduction generally increased with plant size for *A. psilostachya*, with few size-independent differences between individuals grown in habitats with and without bison. Number of male flowers (Figure 2.1), number of female flowers (Figure 2.2.), and total sexual reproductive biomass (Figure 2.4) per individual were all significantly positively correlated with plant size, and those relationships were not significantly different between individuals grown in habitats with and without bison. SRE was positively correlated with aboveground biomass for individuals grown in habitats without bison, but there was no significant linear relationship between those variables for individuals grown in habitats with bison. Both aboveground biomass and the presence of bison were significant predictors of SRE, but there was no significant interaction between the two (Figure 2.3). Individuals grown in bison-present habitats showed greater variability in all measures of size and reproduction than those grown in bison-absent habitats.

Artemisia ludoviciana

Sexual reproduction generally increased with plant size for *A. ludoviciana*, with no size-independent differences between individuals grown in habitats with and without bison. Number of flowers (Figure 2.5), SRE (Figure 2.6), and sexual reproductive biomass (Figure 2.7) were all significantly, positively correlated with plant size. The relationships between those variables and individual size were not significantly different between individuals grown in bison-present and bison-absent habitats.

Baptisia australis

Not all measures of sexual reproduction were significantly correlated with plant size for *B. australis*, and some measures were significantly influenced by the presence of bison. Number of flowers, and sexual reproductive biomass were both significantly, positively correlated with plant size. Both aboveground biomass and presence of bison in habitat were significant predictors of number of flowers, but there was no significant interaction between the two (Figure 2.8). The relationships between sexual reproductive mass and individual size were not significantly different between individuals grown in bison-present and bison-absent habitats (Figure 2.10). There was no significant linear relationship between plant size and SRE for either population; the presence of bison was a significant predictor of SRE, but neither plant size nor its interaction with bison's presence was a significant model component (Figure 2.9). There was little overlap in range of measures of size and reproduction between individuals grown in habitats with and without bison.

Vegetative reproduction showed little relationship with plant size for *B. australis*. Number of rhizomes was significantly, positively correlated with plant size, and the slope of this relationship was significantly different between bison-present and bison-absent habitats (Figure 2.11). There were no significant linear relationships between plant size and VRE (Figure 2.12) or mass of rhizomes (Figure 2.13), nor were there any significant differences between individuals grown in habitats with and without bison.

Psoralidium tenuiflorum

Sexual reproduction generally increased with size for *P. tenuiflorum*, with some differences in relationships between bison-present and bison-absent habitats. Number of fruit was significantly positively correlated with plant size, with no significant differences in the

relationship between individuals grown in bison-present and bison-absent habitats (Figure 2.14). Both aboveground biomass and the presence of bison were significant predictors of SRE, which was positively correlated with plant size but only significantly so in bison-absent habitats (Figure 2.15). Mass of sexual reproductive structures was significantly, positively correlated with aboveground vegetative biomass, and the slope of the relationship was significantly different between bison-present and bison-absent habitats. There was much greater variation in SRE and sexual reproductive mass in bison-present habitats than in bison-absent ones, but both habitats showed similar variation in size.

Solidago canadensis

Sexual reproduction was generally correlated with plant size for *S. canadensis*, with little difference between bison-present and bison-absent habitats. SRE was significantly, positively correlated with aboveground biomass; both size and the presence of bison had significant main effects. There was much greater variation in SRE and size in bison-present habitats than in bison-absent ones (Figure 2.17). Sexual reproductive mass was positively, significantly correlated with aboveground vegetative biomass, with no significant effects of bison presence (Figure 2.18).

Not all measures of vegetative reproduction were significantly correlated with plant size for *S. canadensis*. There was no significant linear relationship between number of rhizomes and plant size, nor were there any significant between-habitat differences (Figure 2.19). There was no significant linear relationship between VRE and aboveground biomass for either habitat's population taken separately, but aboveground biomass had a significant main effect (Figure 2.20). Mass of rhizomes increased significantly with aboveground vegetative biomass, and the relationship was not significantly different between habitats with and without bison (Figure

2.21). Both habitats showed a similar range in measures of vegetative reproduction, but variation in individual size was much greater in bison-present habitats.

This study found no evidence for a trade-off between vegetative and sexual reproduction. There was no significant linear relationship between SRE and VRE for either habitat, although the trend showed a negative slope in both cases (Figure 2.22), nor between sexual reproductive mass and mass of rhizomes in bison-absent habitats. There was a significant, positive linear relationship between sexual and vegetative reproductive masses in bison-present habitats, but this relationship was weak (Figure 2.23). The presence of bison did not seem to significantly affect the relationships between VRE and SRE or between vegetative and sexual reproductive mass, but variation in SRE and sexual reproductive mass were much greater in bison-present habitats.

Vernonia baldwinii

Sexual reproduction was correlated with size, but only in habitats where bison were present. Number of flowers (Figure 2.24), SRE (Figure 2.25), and sexual reproductive mass (Figure 2.26) were all positively, significantly correlated with individual size in bison-present habitats, and all three relationships were significantly different between bison-present and bison-absent habitats. There was no significant linear relationship between any measure of sexual reproduction and size in bison-absent habitats. Bison-present habitats showed a much greater range in individual size and in all measures of sexual reproduction than bison-absent habitats.

Vegetative reproduction did not show any clear pattern in relationships with size, and all three variables showed significantly different relationships with size between habitats with and without bison. There was a positive, significant linear relationship between number of rhizomes and aboveground biomass, and this relationship differed significantly between habitats with and

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without bison (Figure 2.27). VRE was significantly, negatively correlated with aboveground biomass, but only in bison-present habitats (Figure 2.27). Conversely, only in bison-absent habitats was there a significant, positive linear relationship between mass of rhizomes and aboveground vegetative mass (Figure 2.28). Plant size showed much greater variation in bison-present habitats, but variation in measures of vegetative reproduction was not as clearly different between habitats.

There was no evidence for a trade-off between sexual and vegetative reproduction regardless of whether bison were present in the habitat. Neither SRE and VRE (Figure 2.30) nor sexual and vegetative reproductive mass (Figure 2.31) showed any significant linear relationships for either habitat. Variation in SRE and in sexual reproductive mass were both much greater in habitats with bison, but range in measures of vegetative reproduction was not so clearly different.

Discussion

Sexual Reproduction

For most of the species and habitats represented in this study, plant size was a significant predictor of sexual reproductive output. Most species appeared to have a size threshold for sexual reproduction. The relationship between size and sexual reproduction differed significantly between habitats for at least one measure for all species except *A. ludoviciana*, which is consistent with earlier findings that neither size nor reproduction is significantly different between bison-grazed and ungrazed habitats for this species (Chapter 1). Out of the 34 relationships between size and sexual reproduction tested, only nine had $r^2 > 0.5$, and r^2 was always $< .5$ for three of the species studied, indicating that a large proportion of variability in sexual reproduction cannot be explained by differences in size alone.

The number of flowers or fruits produced per individual was significantly and positively correlated with total aboveground biomass for five out of five species in bison-grazed habitats and for all species except *V. baldwinii* in ungrazed habitats. The relationship was significantly different between habitat types for two species: *B. australis* and *V. baldwinii*. For *B. australis*, number of flowers may be the most accurate estimator of reproductive allocation since such a large proportion of the flowers and fruits were consumed by *Epicauta* sp. (blister beetles) that rachis mass had to be substituted for sexual reproductive mass for the other calculations. Flower maturation and production for *V. baldwinii* was suppressed by weather conditions in later-blooming individuals, including all individuals in ungrazed habitats but only a few in bison-grazed habitats, contributing to large differences in patterns of allocation to sexual reproduction for this species.

There was a positive, significant relationship between total aboveground biomass and SRE for three out of six species in bison-grazed habitats and for four out of six species in ungrazed habitats. The relationship was significantly different between bison-grazed and ungrazed habitats for all species (except *A. ludoviciana*), indicating that differences in sexual reproductive allocation are not explained solely by plant size and thus also may be due to adaptive phenotypic responses to the differences in habitat conditions. There was no significant relationship between SRE and total aboveground biomass for *B. australis* in either habitat, possibly because insect herbivory had such a strong impact on allocation to sexual reproduction for that species (Chapter 1).

There was a positive, significant linear relationship between total mass (g) of sexual reproductive parts and total mass (g) of aboveground vegetative structures for all six species in bison-grazed habitats and for all species except *V. baldwinii* in ungrazed habitats. The relationship was significantly different between habitats for *P. tenuiflorum*, *B. australis*, and *V. baldwinii*. So, both reproductive and vegetative mass contribute to variation in SRE for the species studied. This relationship, along with changes in flower/fruit number with size, indicates that these species are capable of increasing reproductive output and size plastically. It is important to note that this is not always the case, since changes in SRE in some species are caused by changes in vegetative biomass with constant reproductive biomass, or vice versa.

Variability in both size and sexual reproduction were both generally greater in bison-grazed habitats, which is consistent with the greater environmental heterogeneity expected in that habitat. Thus, though differences in size of aboveground tissues likely contributes to some of the differences in sexual reproduction between bison-grazed and ungrazed habitats, the differences in reproduction between habitats are not entirely size-dependent.

Vegetative Reproduction

Plant size, as measured by aboveground biomass, was not a reliable indicator of vegetative reproductive output. No species seemed to have a size threshold for vegetative reproduction. None of the significant relationships between measures of vegetative reproduction and aboveground size had $r^2 > .5$, indicating that a large proportion of the observed variation in vegetative reproduction was not explained by plant size.

There was a positive, significant correlation between plant size and number of rhizome buds for two out of the three species studied, and the relationship was significantly different between grazed and ungrazed habitats for *B. australis*. Since each rhizome bud is a potential vegetative offspring, number of rhizome buds could be considered analogous to seed number.

There was no relationship between VRE and aboveground biomass except for individuals of *V. baldwinii* in bison-grazed habitats, for whom the relationship was weak and negative. This weak decrease in VRE is likely due to a lack of increase in rhizome bud mass with increases in aboveground vegetative mass rather than to a reduction in vegetative reproductive output.

There was a significant, positive relationship between aboveground vegetative biomass and total mass of rhizome buds for two species in ungrazed habitats and for one species in bison-grazed habitats; the relationships were significantly different for one species, *V. baldwinii*. So, variation in VRE was mostly driven by changes in vegetative mass for *B. australis* and for *V. baldwinii* in bison-grazed habitats, but changes in both reproductive and vegetative mass contributed to variation in VRE for *S. canadensis* and for *V. baldwinii* in ungrazed habitats.

Thus, there does not seem to be a very strong link between aboveground size and vegetative reproduction, nor is there a clear pattern of bison's presence significantly affecting vegetative reproduction in the species studied. Other studies have failed to find a relationship between allocation to vegetative reproduction and individual size (Hartnett 1990; Mendoza &

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Franco 1998). Perhaps including the masses of other belowground structures such as roots would help better explain variation in vegetative reproduction, but this was not possible in this study since extracting all root biomass from the rocky, clay-heavy soils of Konza Prairie Biological Station was unfeasible. This study assumed that rhizome production by time of peak flower for the species studied would be a representative sample of end-of-season rhizome production; further study is needed to determine if this assumption is valid. More studies of the factors influencing rhizome bud production are necessary since recruitment from vegetative buds is far higher than recruitment from seed for many tallgrass prairie species (Benson et al. 2004).

No Trade-off between Sexual and Vegetative Reproduction

There was no evidence of any within-individual trade-offs between sexual and vegetative reproduction. A negative relationship between VRE and SRE or between total mass of rhizome buds and total mass of sexual reproductive structures would have indicated a trade-off in allocation between vegetative and sexual reproduction, but such a relationship was not observed for either species. There was no significant linear relationship between VRE and SRE for either of the two species studied. The only significant linear relationship between total masses of rhizome buds and of sexual reproductive structures was for *S. canadensis* individuals grown in bison-grazed habitats; however, this relationship was weak and positive, providing no evidence for a trade-off.

As mentioned above and in Chapter 1, allocation to sexual reproduction was suppressed by weather conditions for all late-blooming individuals, including all individuals in ungrazed habitats and a few in bison-grazed habitats, providing a sort of natural experiment. If there was a trade-off between allocation to vegetative and sexual reproduction, individuals for which sexual reproductive allocation was suppressed would be expected to increase allocation to vegetative

reproduction, assuming that the weather conditions were not also inhibitory to rhizome bud production. However, individuals for whom sexual reproductive allocation was suppressed did not seem to allocate more to vegetative reproduction than similarly-sized individuals for which sexual reproduction was not suppressed. Though this natural experiment of sorts leaves too many variables to chance to provide definitive proof that there is not a trade-off between vegetative and sexual reproductive allocation for *V. baldwinii*, it certainly does not provide evidence supporting the existence of a trade-off.

Thus, this study found no evidence supporting the notion that there is a trade-off between allocation to sexual and vegetative reproduction. These findings are consistent with those of some other studies of reproductive allocation in clonal plants (Mendoza & Franco 1998; Schulze et al 2012). Some have suggested that the growth of vegetative reproductive structures may be regulated more similarly to the growth of non-reproductive vegetative structures than to sexual reproductive allocation (Schmid et al. 1995). The lack of a relationship between measures of sexual and vegetative reproduction and the differences in their responses to size (increasing vs. unrelated) and to the presence of bison (greater on average vs. not different, Chapter 1) together indicate that there are large differences in how allocation to sexual and vegetative reproduction are regulated in these species.

Conclusion

In summary, this study found evidence that differences in reproduction between bison-grazed and ungrazed habitats are not entirely size-dependent. Aboveground biomass was generally positively correlated with sexual reproduction, but much of the variability was unexplainable by differences in size alone. Vegetative reproduction was not necessarily linked to aboveground biomass, nor was there a clear trade-off between sexual and vegetative

reproduction, potentially indicating that allocation to vegetative reproduction may be regulated differently than allocation to sexual reproduction. A variety of size-independent factors, such as variation in insect herbivory, resource availability, competition, and genes regulating reproductive allocation could potentially be causing shifts in individual allocation to sexual reproduction independent of size, and differences in these factors between bison-grazed and ungrazed habitats could potentially contribute to differences in sexual reproduction.

Figures and Tables

Table 2.1 All species: Number of individuals sampled and percentage of sampled individuals that produced flowers.

Species	# of Individuals Sampled		% Flowering	
	Bison-Present	Bison-Absent	Bison-Present	Bison-Absent
A. psilostachya	35	32	97.1	81.3
A. ludoviciana	35	33	65.7	39.4
B. australis	29	31	86.2	29.0
P. tenuiflorum	30	30	93.3	86.7
S. canadensis	32	33	87.5	51.5
V. baldwinii	30	30	80.0	16.7
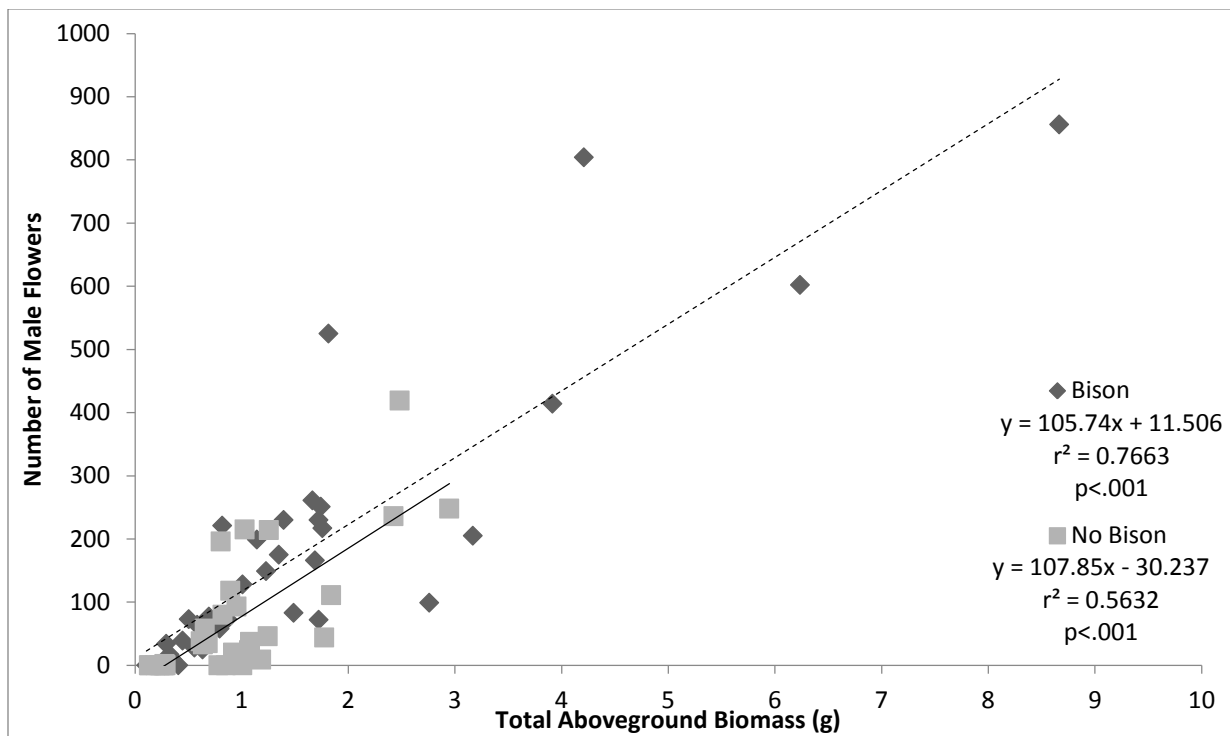
Figure 2.1 *Ambrosia psilostachya:* Relationship between number of male flowers produced and total aboveground biomass (g) for individuals grown in habitats with and without bison.

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.759, p<.001; main effects: Size p<.001, Grazing p=.222, Size*Grazing p=.932.
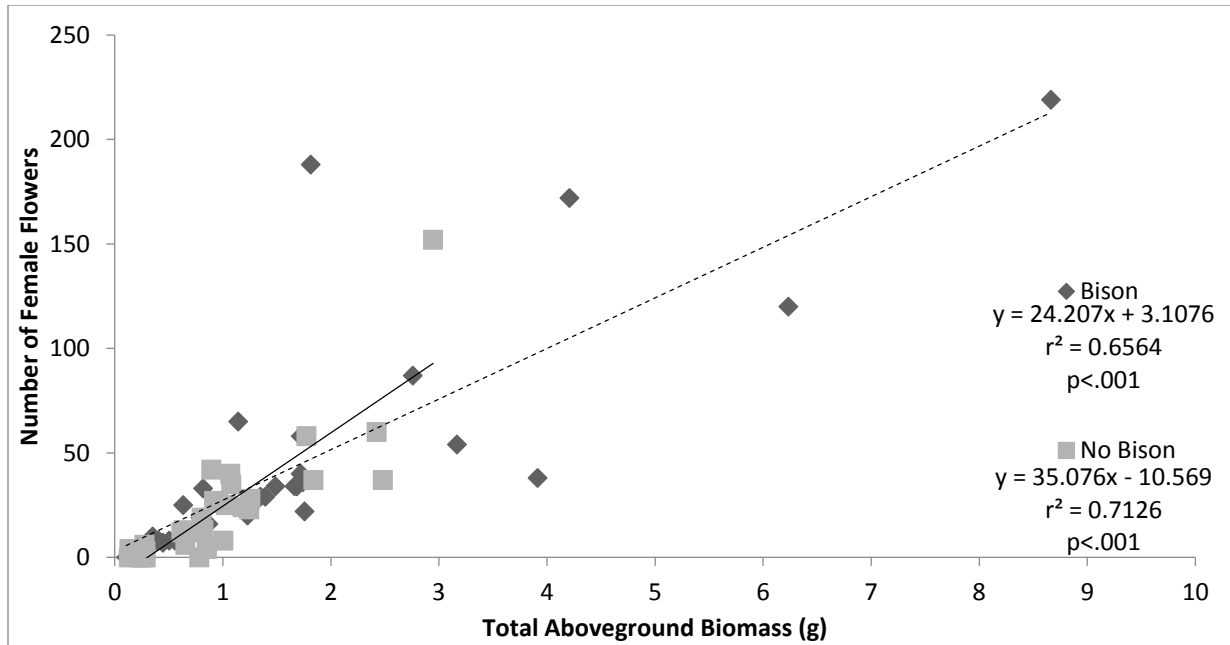
Figure 2.2 *Ambrosia psilostachya***: Relationship between number of female flowers produced and total aboveground biomass (g) for individuals grown in habitats with and without bison.**

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.685, p<.001; main effects: Size p<.001, Grazing p=.123, Size*Grazing p=.123.
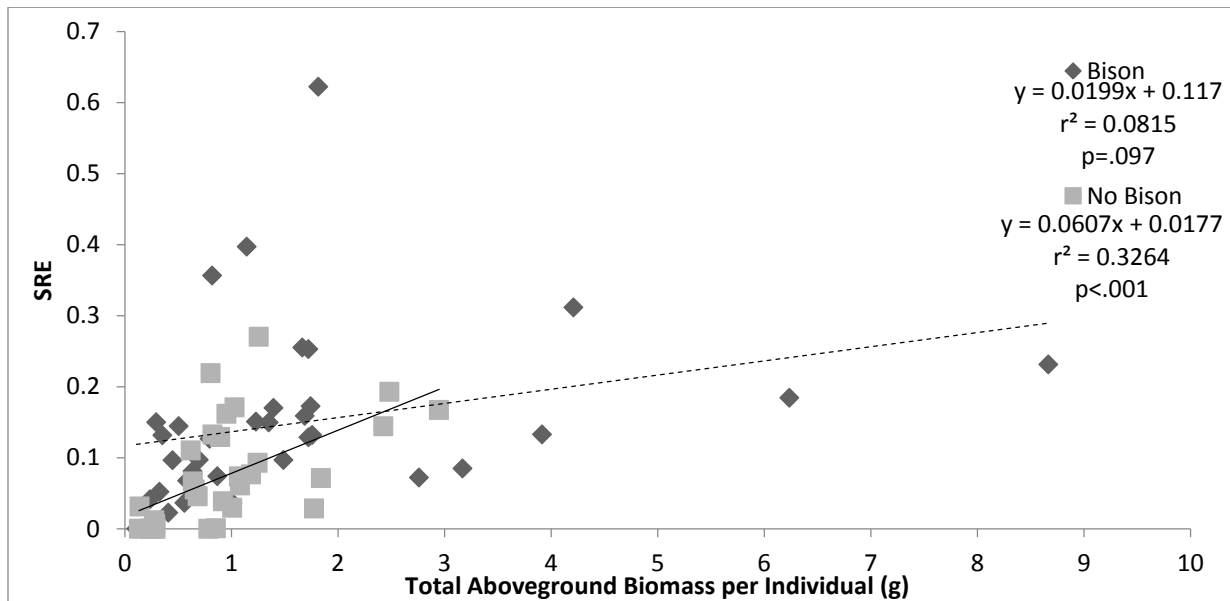

Figure 2.3 *Ambrosia psilostachya***: Relationship between SRE and aboveground biomass (g) for individuals grown in habitats with and without bison.**

Sexual Reproductive Effort (SRE) was calculated as the ratio of the total mass (g) of sexual reproductive structures to the total mass (g) of aboveground stems and leaves produced by each individual. The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.242, p<.001; main effects: Size p=.004, Grazing p=.009, Size*Grazing p=.132.
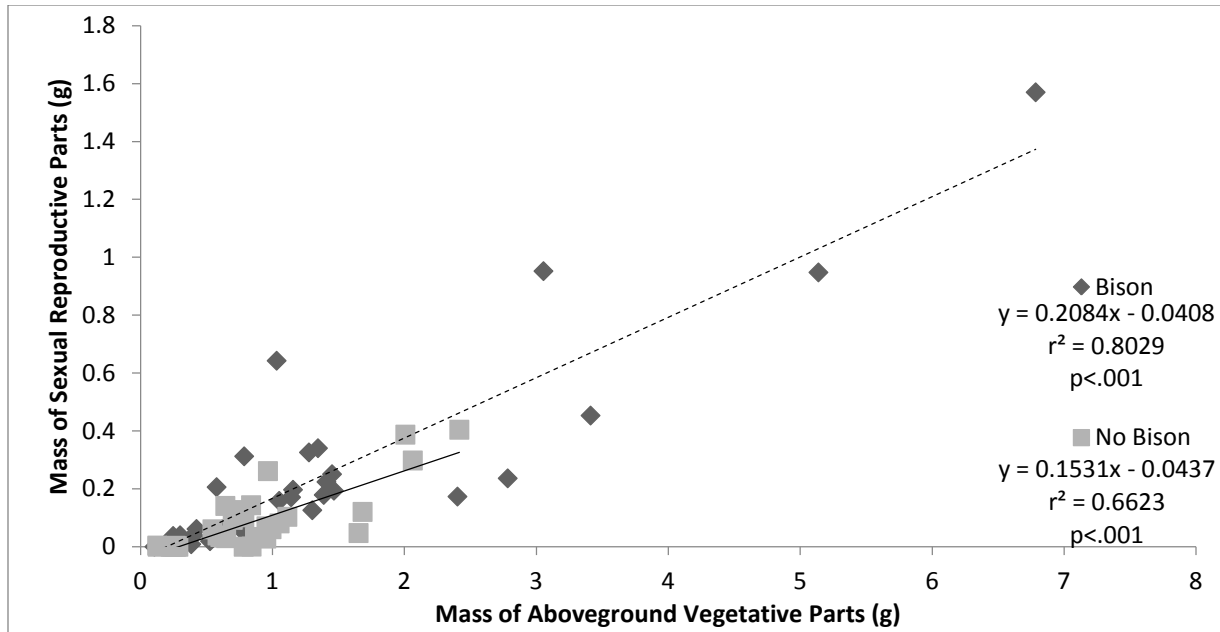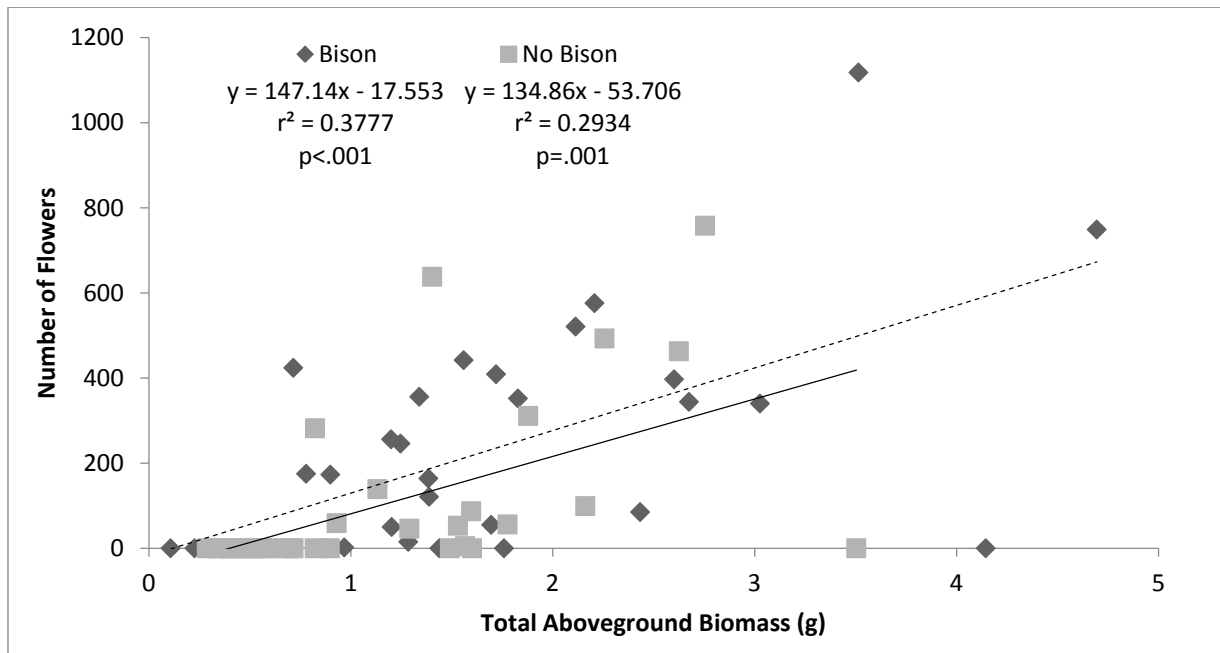
Figure 2.4 *Ambrosia psilostachya*: Relationship between total masses (g) of sexual reproductive and aboveground vegetative parts for individuals grown in habitats with and without bison.

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.808, p<.001; main effects: Size p<.001, Grazing p=.949, Size*Grazing p=.158.

Figure 2.5 *Artemisia ludoviciana*: Relationship between number of flowers produced and total aboveground biomass (g) for individuals grown in habitats with and without bison.

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.380, p<.001; main effects: Size p<.001, Grazing p=.663, Size*Grazing p=.813.
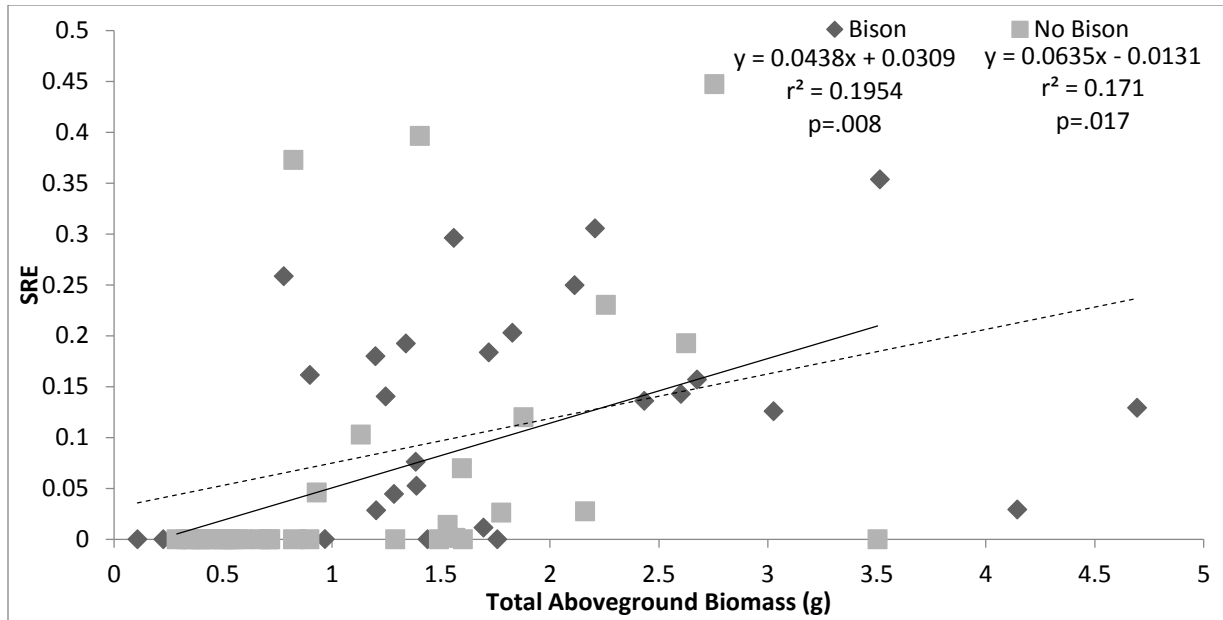
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Figure 2.6 *Artemisia ludoviciana***: Relationship between SRE and aboveground biomass (g) for individuals grown in habitats with and without bison.**

Sexual Reproductive Effort (SRE) was calculated as the ratio of the total mass (g) of sexual reproductive structures to the total mass (g) of aboveground stems and leaves produced by each individual. The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.202, p=.002; main effects: Size p<.001, Grazing p=.342, Size*Grazing p=.495.
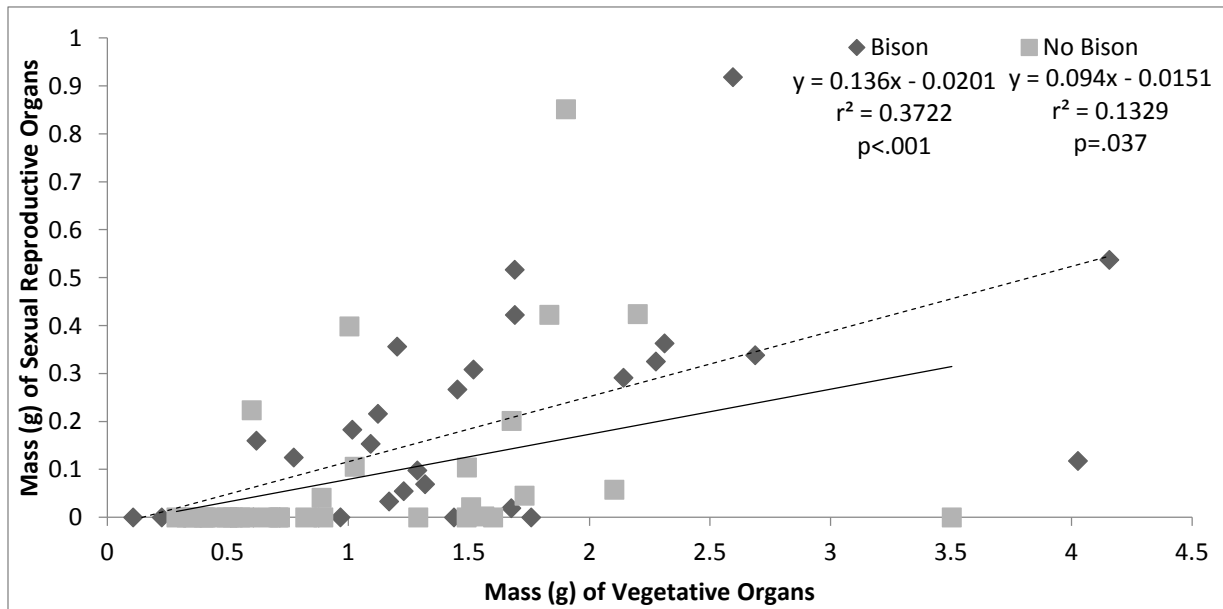

Figure 2.7 *Artemisia ludoviciana***: Relationship between total masses (g) of sexual reproductive and aboveground vegetative parts for individuals grown in habitats with and without bison.**

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.300, p<.001; main effects: Size p<.001, Grazing p=.947, Size*Grazing p=.429.
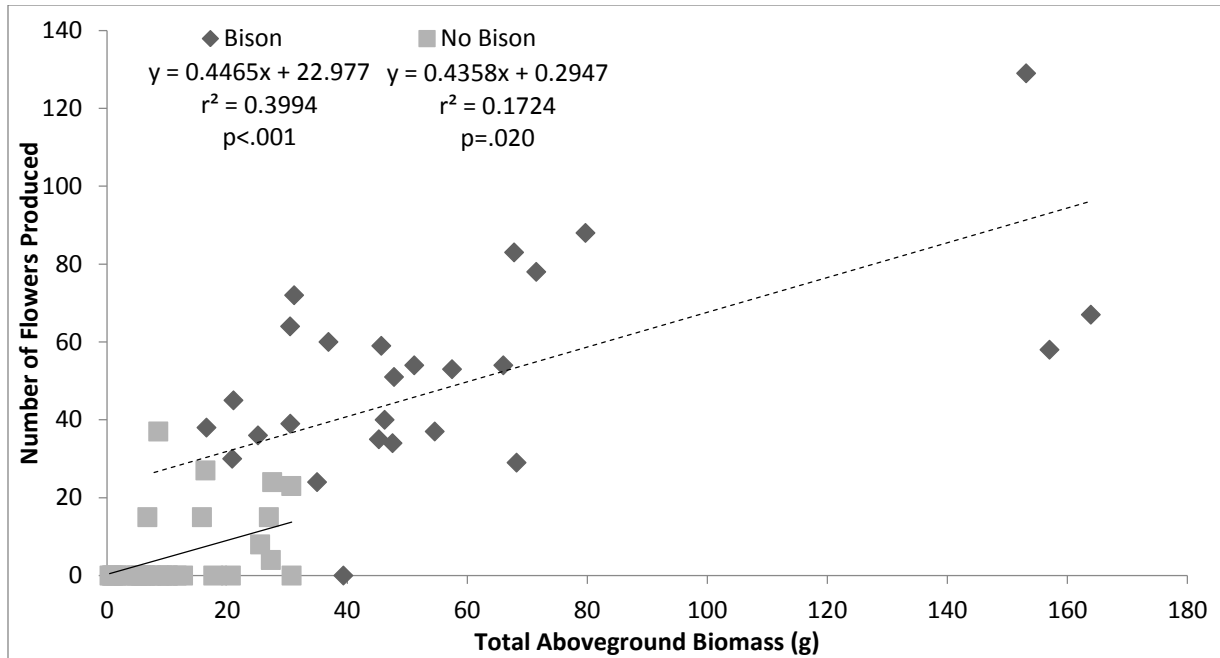
Figure 2.8 *Baptisia australis***: Relationship between number of flowers produced and total aboveground biomass (g) for individuals grown in habitats with and without bison.**

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.683, p<.001; main effects: Size p=.011, Grazing p=.002, Size*Grazing p=.975.
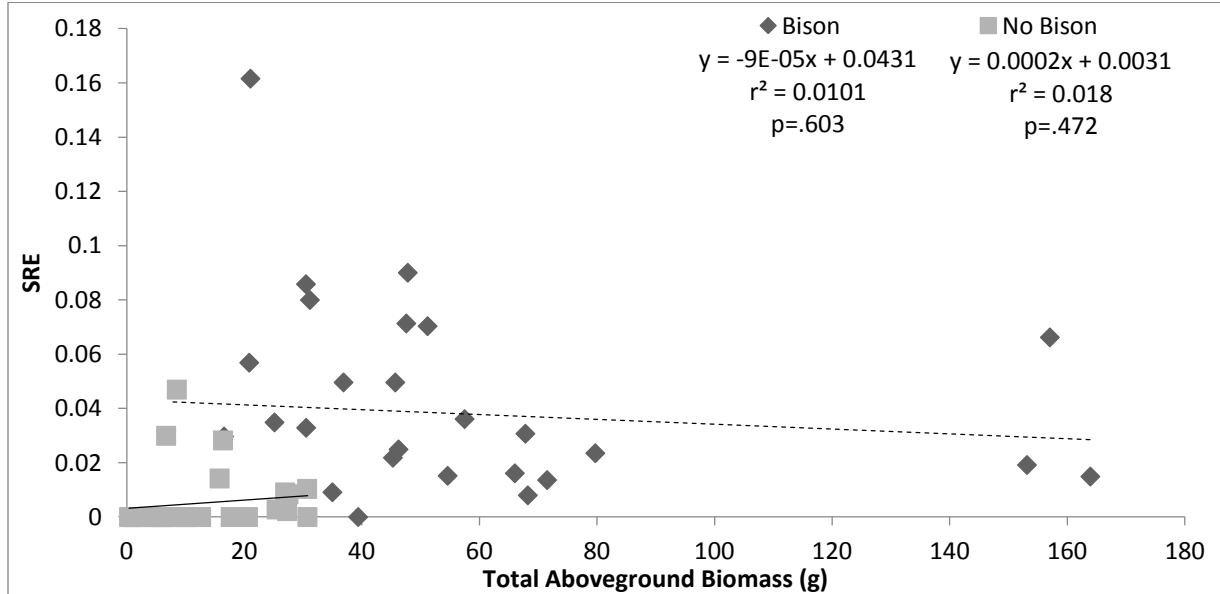

Figure 2.9 *Baptisia australis***: Relationship between SRE and aboveground biomass (g) for individuals grown in habitats with and without bison.**

Sexual Reproductive Effort (SRE) was calculated as the ratio of the total mass (g) of sexual reproductive structures to the total mass (g) of aboveground stems and leaves produced by each individual. The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.303, p<.001; main effects: Size p=.902, Grazing p<.001, Size*Grazing p=.643.
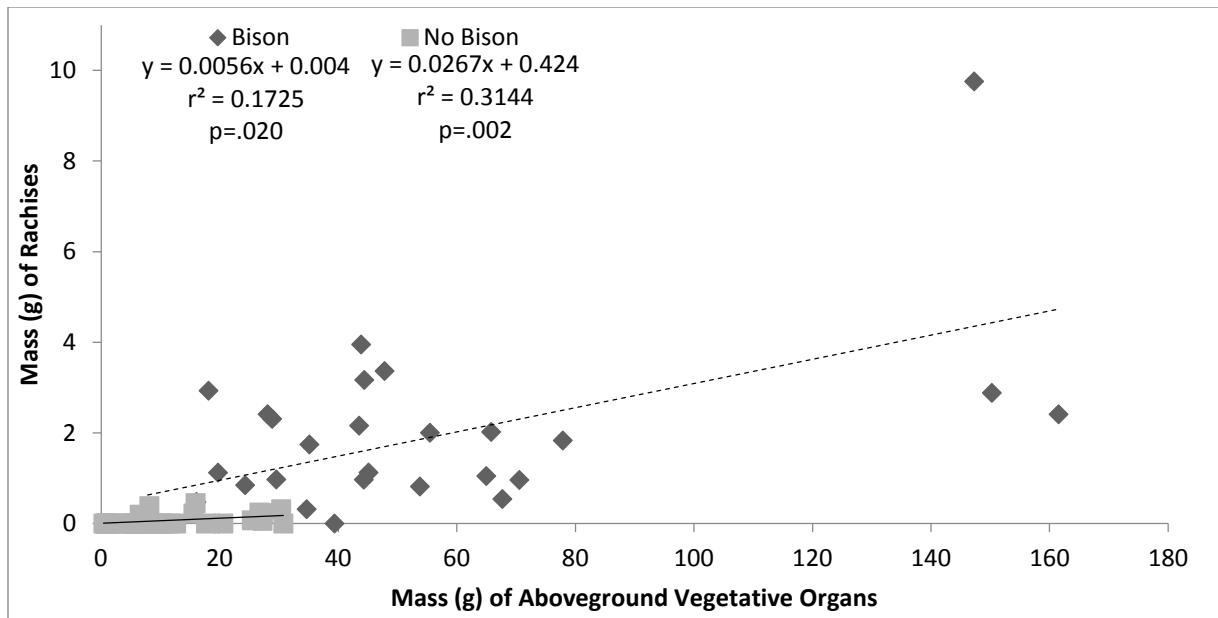
Figure 2.10 *Baptisia australis***: Relationship between total masses (g) of sexual reproductive and aboveground vegetative parts for individuals grown in habitats with and without bison.**

The ANCOVA model was significant despite having no significant coefficients. The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.525, p<.001; main effects: Size p=.145, Grazing p=.371, Size*Grazing p=.340.
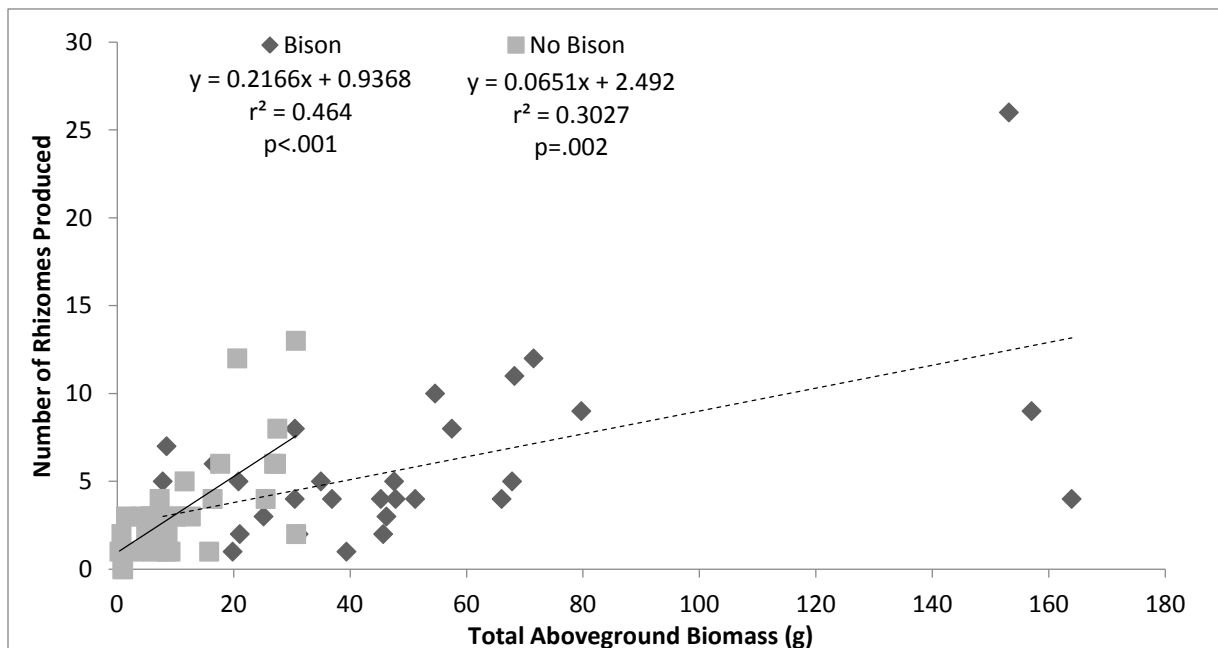

Figure 2.11 *Baptisia australis***: Relationship between number of rhizomes produced and total aboveground biomass (g) for individuals grown in habitats with and without bison.**

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.410, p<.001; main effects: Size p<.001, Grazing p=.583, Size*Grazing p=.022.
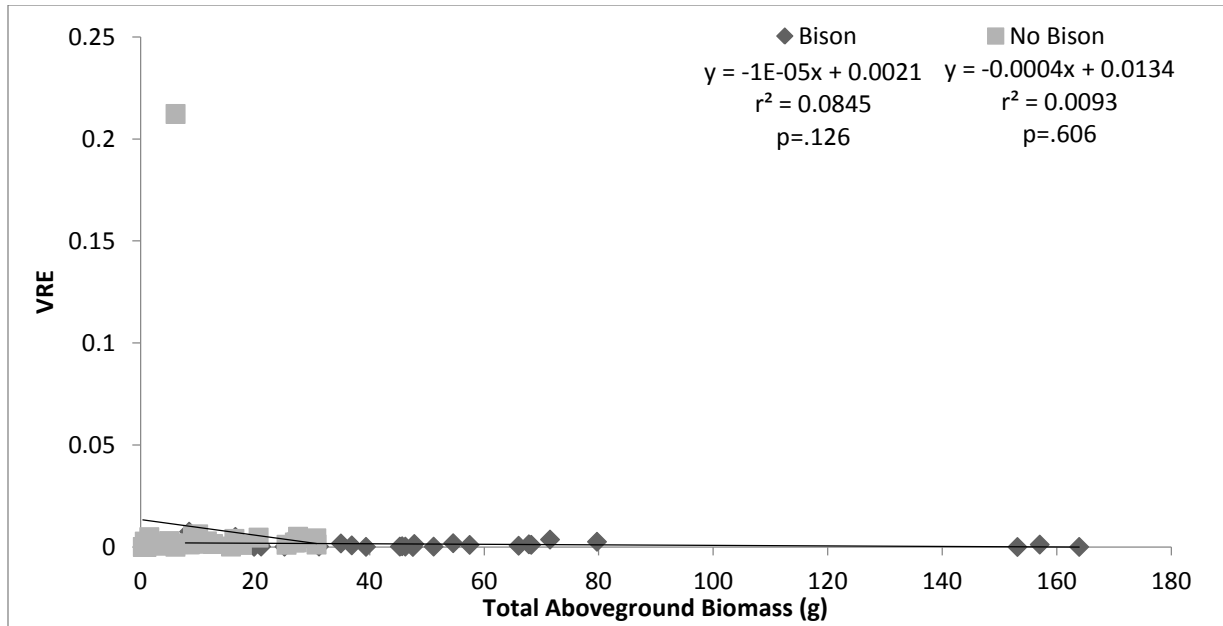
Figure 2.12 *Baptisia australis*: Relationship between VRE and aboveground biomass (g) for individuals grown in habitats with and without bison.

Vegetative Reproductive Effort (VRE) was calculated as the ratio of the total mass (g) of rhizomes to the total mass (g) of aboveground stems and leaves produced by each individual. The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.028, p=.648; main effects: Size p=.470, Grazing p=.332, Size*Grazing p=.499.
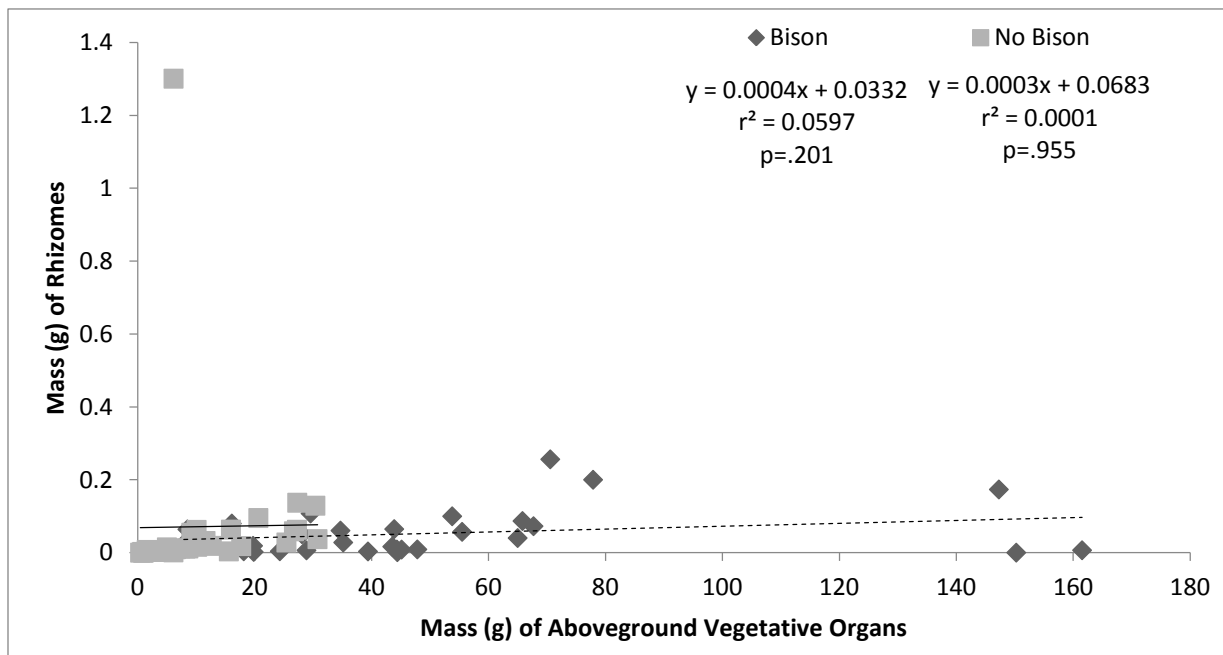

Figure 2.13 *Baptisia australis*: Relationship between total masses (g) of rhizomes and aboveground vegetative parts for individuals grown in habitats with and without bison.

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.007, p=.943; main effects: Size p=.851, Grazing p=.634, Size*Grazing p=.969.
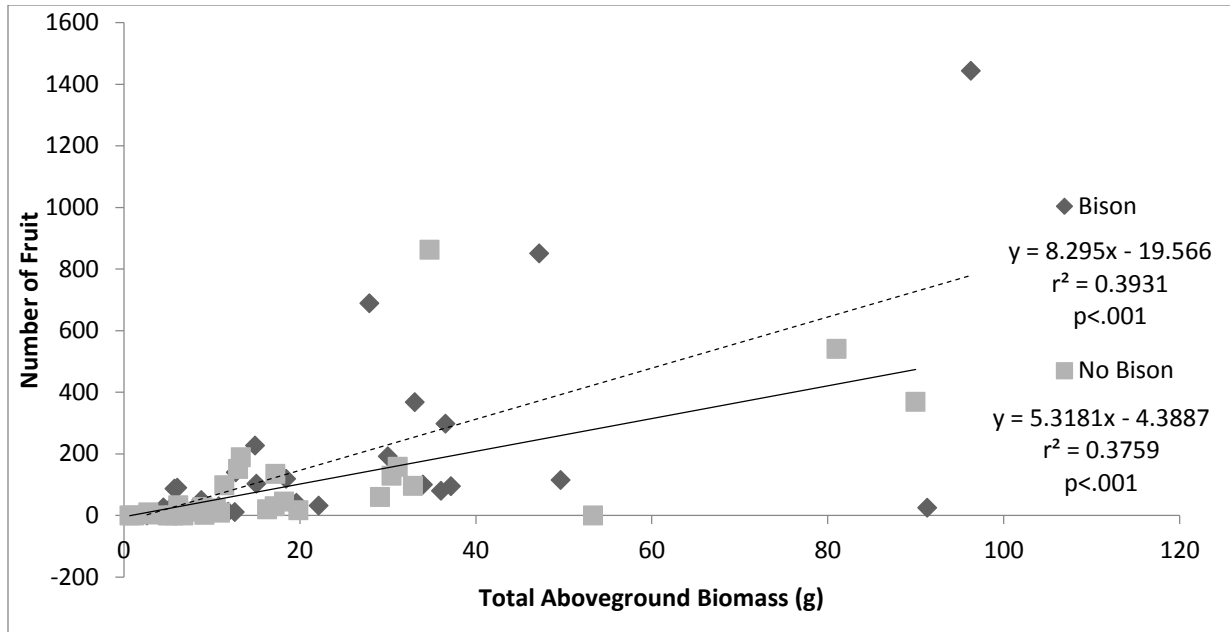
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Figure 2.14 *Psoralidium tenuiflorum*: **Relationship between number of fruit produced and total aboveground biomass (g) for individuals grown in habitats with and without bison.**

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.404, p<.001; main effects: Size p<.001, Grazing p=.840, Size*Grazing p=.220.
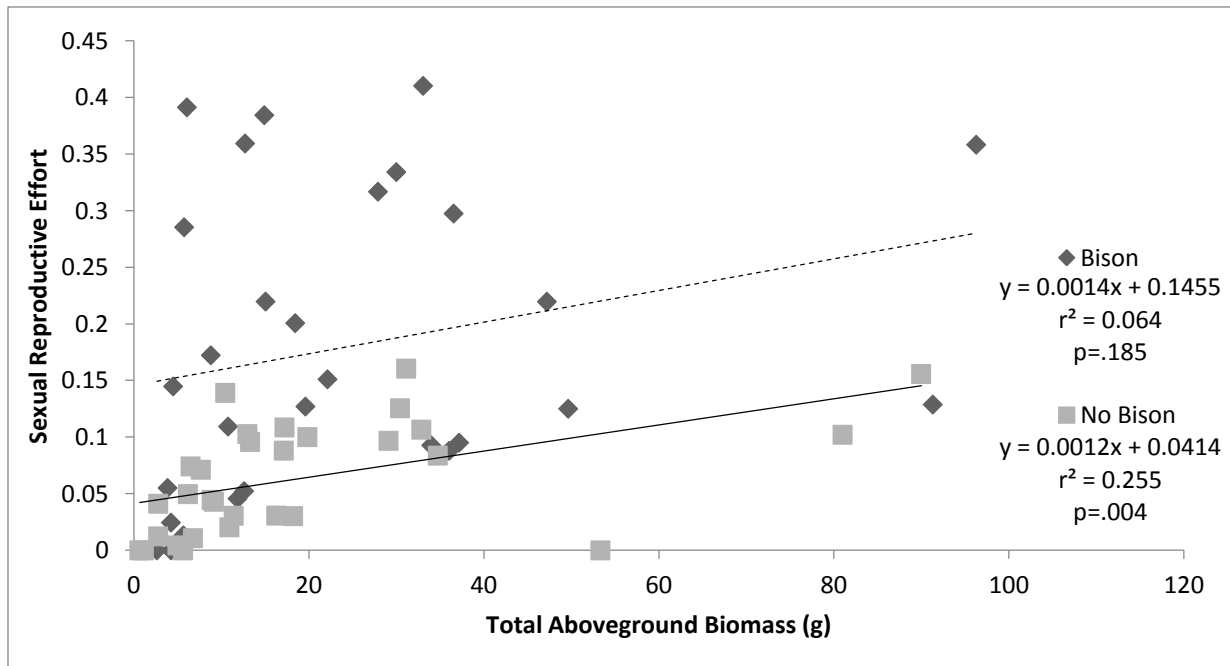

Figure 2.15 *Psoralidium tenuiflorum*: **Relationship between SRE and aboveground biomass (g) for individuals grown in habitats with and without bison.**

Sexual Reproductive Effort (SRE) was calculated as the ratio of the total mass (g) of sexual reproductive structures to the total mass (g) of aboveground stems and leaves produced by each individual. The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.327, p<.001; main effects: Size p=.027, Grazing p=.004, Size*Grazing p=.829.
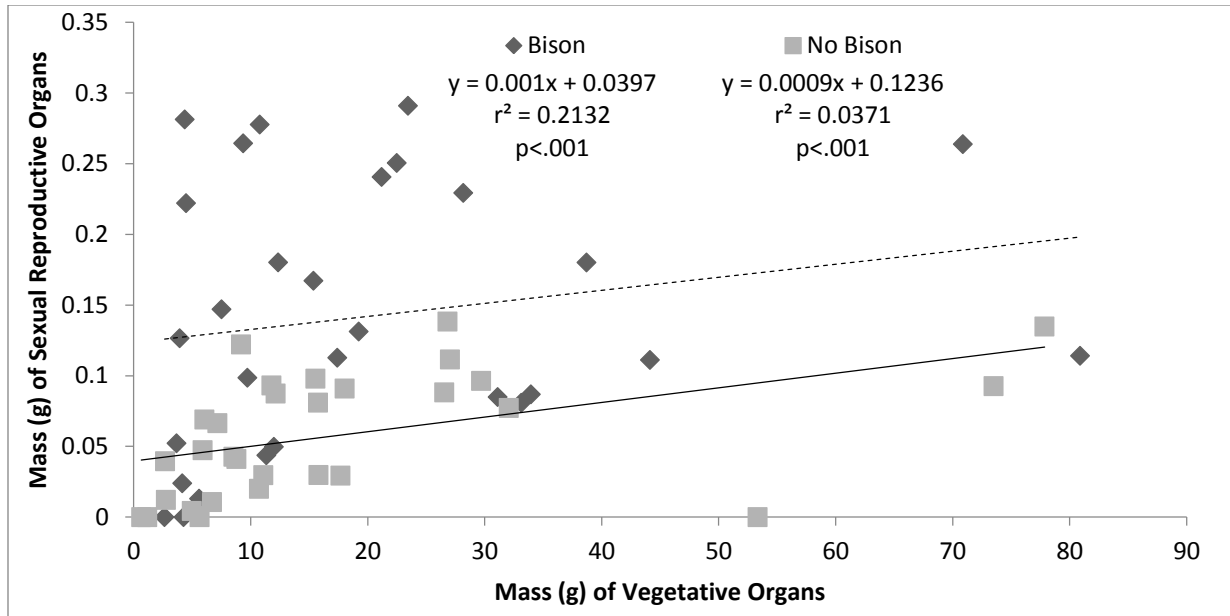
Figure 2.16 *Psoralidium tenuiflorum*: **Relationship between total masses (g) of sexual reproductive and aboveground vegetative parts for individuals grown in habitats with and without bison.**

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.681, p<.001; main effects: Size p<.001, Grazing p=.799, Size*Grazing p=.005.
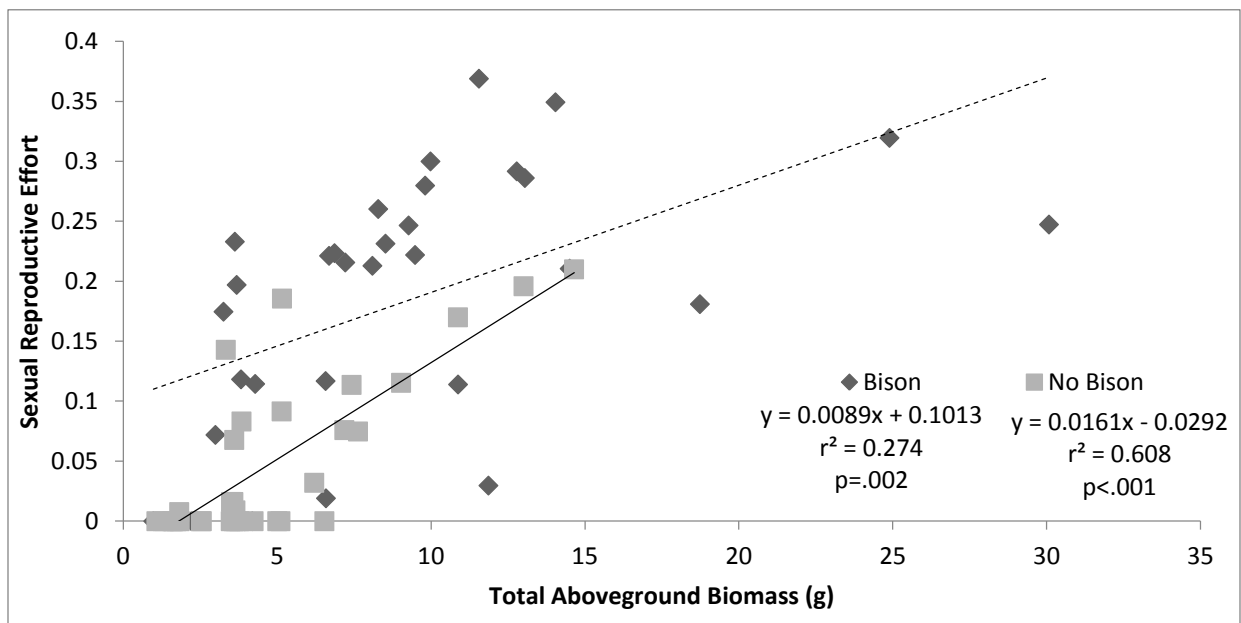

Figure 2.17 *Solidago canadensis*: **Relationship between SRE and aboveground biomass (g) for individuals grown in habitats with and without bison.**

Sexual Reproductive Effort (SRE) was calculated as the ratio of the total mass (g) of sexual reproductive structures to the total mass (g) of aboveground stems and leaves produced by each individual. The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.598, p<.001; main effects: Size p<.001, Grazing p<.001, Size*Grazing p=.110.
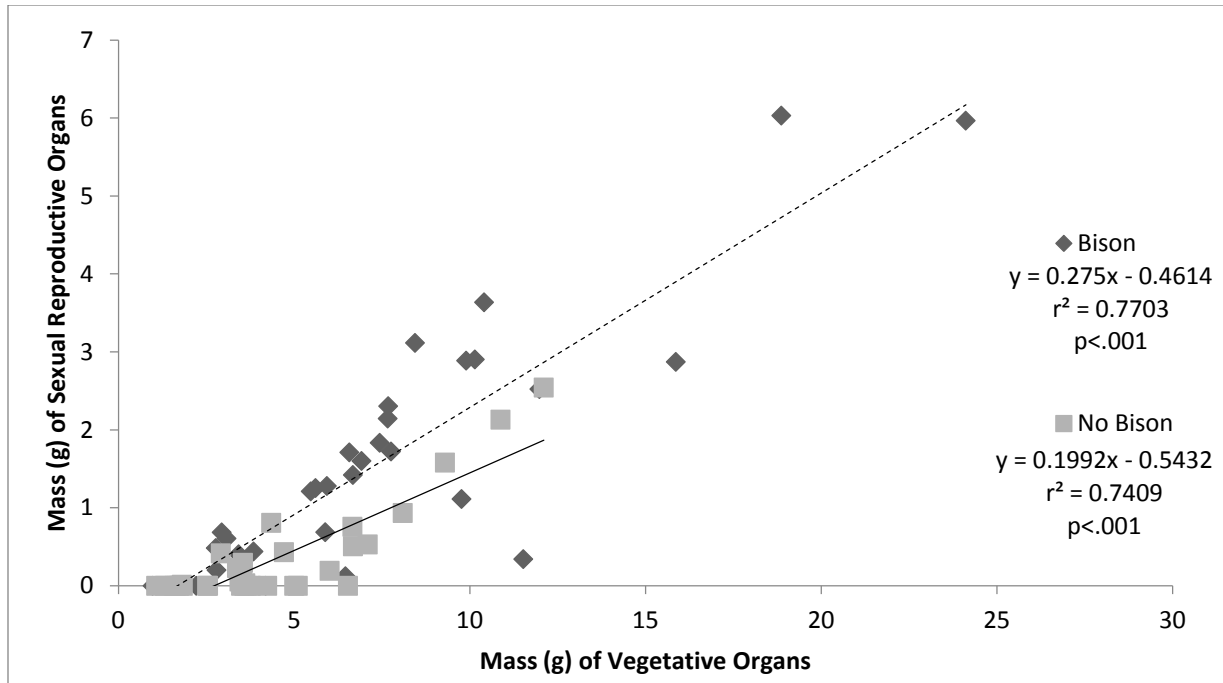
Figure 2.18 *Solidago canadensis***: Relationship between total masses (g) of sexual reproductive and aboveground vegetative parts for individuals grown in habitats with and without bison.**

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.819, p<.001; main effects: Size p<.001, Grazing p=.765, Size*Grazing p=.084.
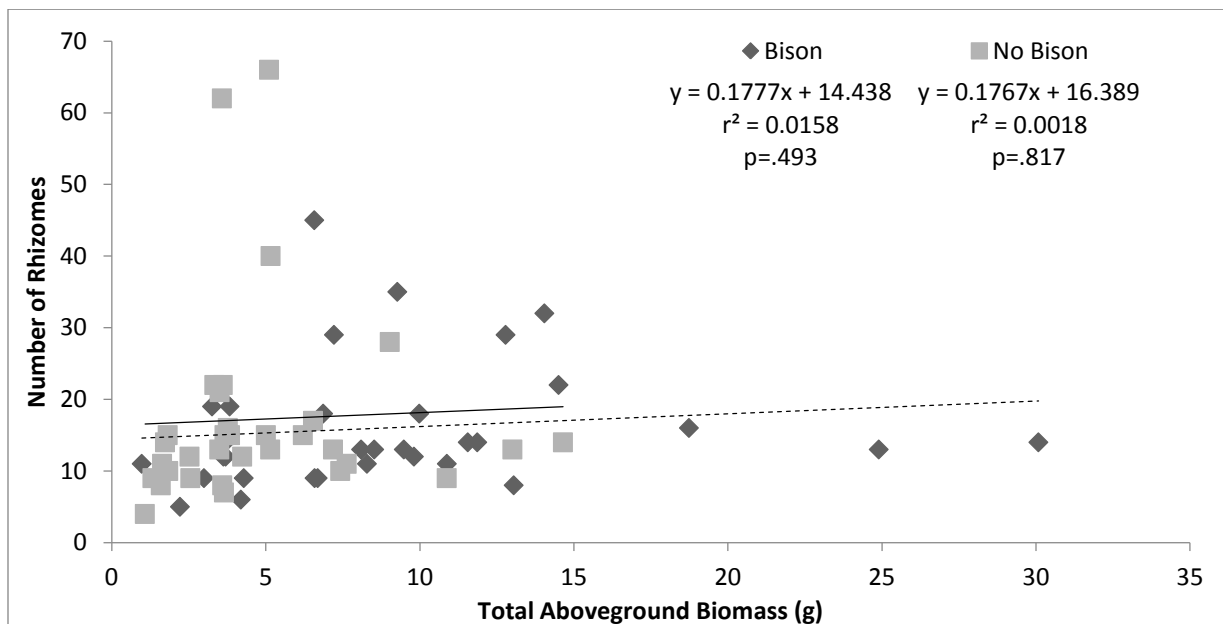

Figure 2.19 *Solidago canadensis***: Relationship between number of rhizomes produced and total aboveground biomass (g) for individuals grown in habitats with and without bison.**

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.008, p=.914; main effects: Size p=.625, Grazing p=.711, Size*Grazing p=.999.
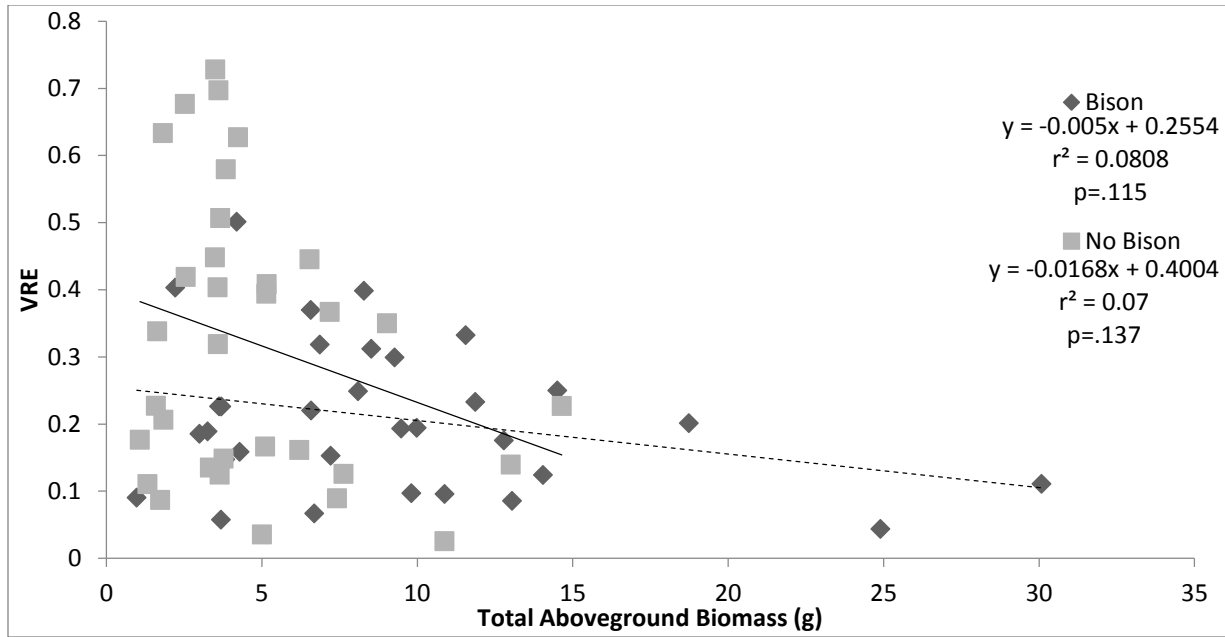
Figure 2.20 *Solidago canadensis***: Relationship between VRE and aboveground biomass (g) for individuals grown in habitats with and without bison.**

Vegetative Reproductive Effort (VRE) was calculated as the ratio of the total mass (g) of rhizomes to the total mass (g) of aboveground stems and leaves produced by each individual. The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.164, p=.012; main effects: Size p=.033, Grazing p=.051, Size*Grazing p=.242.
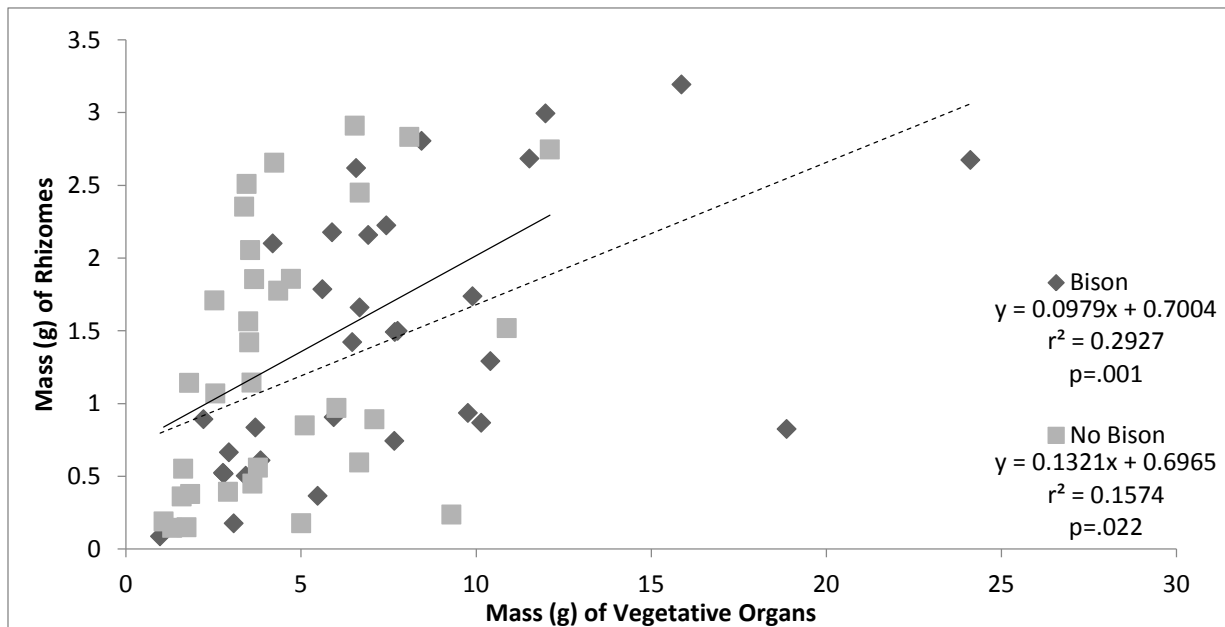

Figure 2.21 *Solidago canadensis***: Relationship between total masses (g) of rhizomes and aboveground vegetative parts for individuals grown in habitats with and without bison.**

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.229, p<.001; main effects: Size p<.001, Grazing p=.992, Size*Grazing p=.572.

Figure 2.22 *Solidago canadensis***: Relationship between SRE and VRE for individuals grown in habitats with and without bison.**

Sexual Reproductive Effort (SRE) was calculated as the ratio of the total mass (g) of sexual reproductive structures to the total mass (g) of aboveground stems and leaves produced by each individual. Vegetative Reproductive Effort (VRE) was calculated as the ratio of the total mass (g) of rhizomes to the total mass (g) of aboveground stems and leaves produced by each individual. The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.398, p<.001; main effects: VRE p=.062, Grazing p<.001, VRE*Grazing p=.276. ANCOVA r^2=.139, p=.027; main effects: SRE p=.097, Grazing p=.184, SRE*Grazing p=.495.
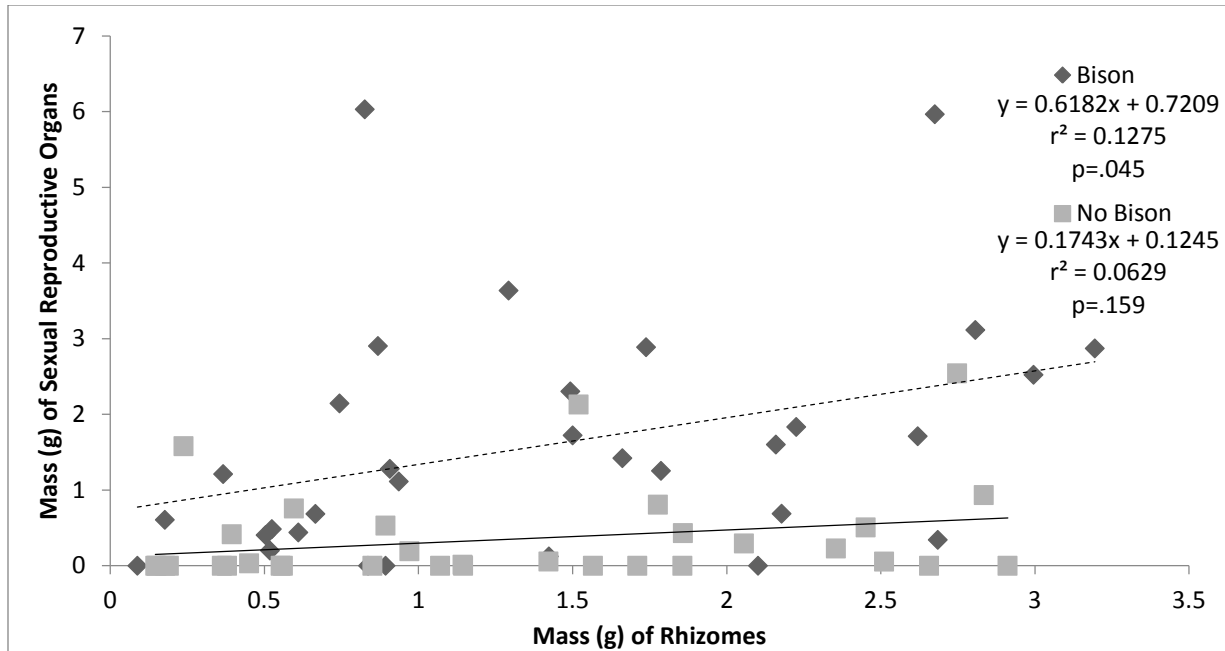
Figure 2.23 *Solidago canadensis***: Relationship between total masses (g) of sexual reproductive organs and rhizomes for individuals grown in habitats with and without bison.**

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.319, p<.001; main effects: Rhizome Mass p=.014, Grazing p=.249, Rhizome Mass*Grazing p=.163. ANCOVA r^2=.101, p=.088; main effects: Floral Mass p=.036, Grazing p=.843, Floral Mass*Grazing p=.562.

Figure 2.24 *Vernonia baldwinii***: Relationship between number of flowers produced and total aboveground biomass (g) for individuals grown in habitats with and without bison.**

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.773, p<.001; main effects: Size p<.001, Grazing p=.279, Size*Grazing p<.001.
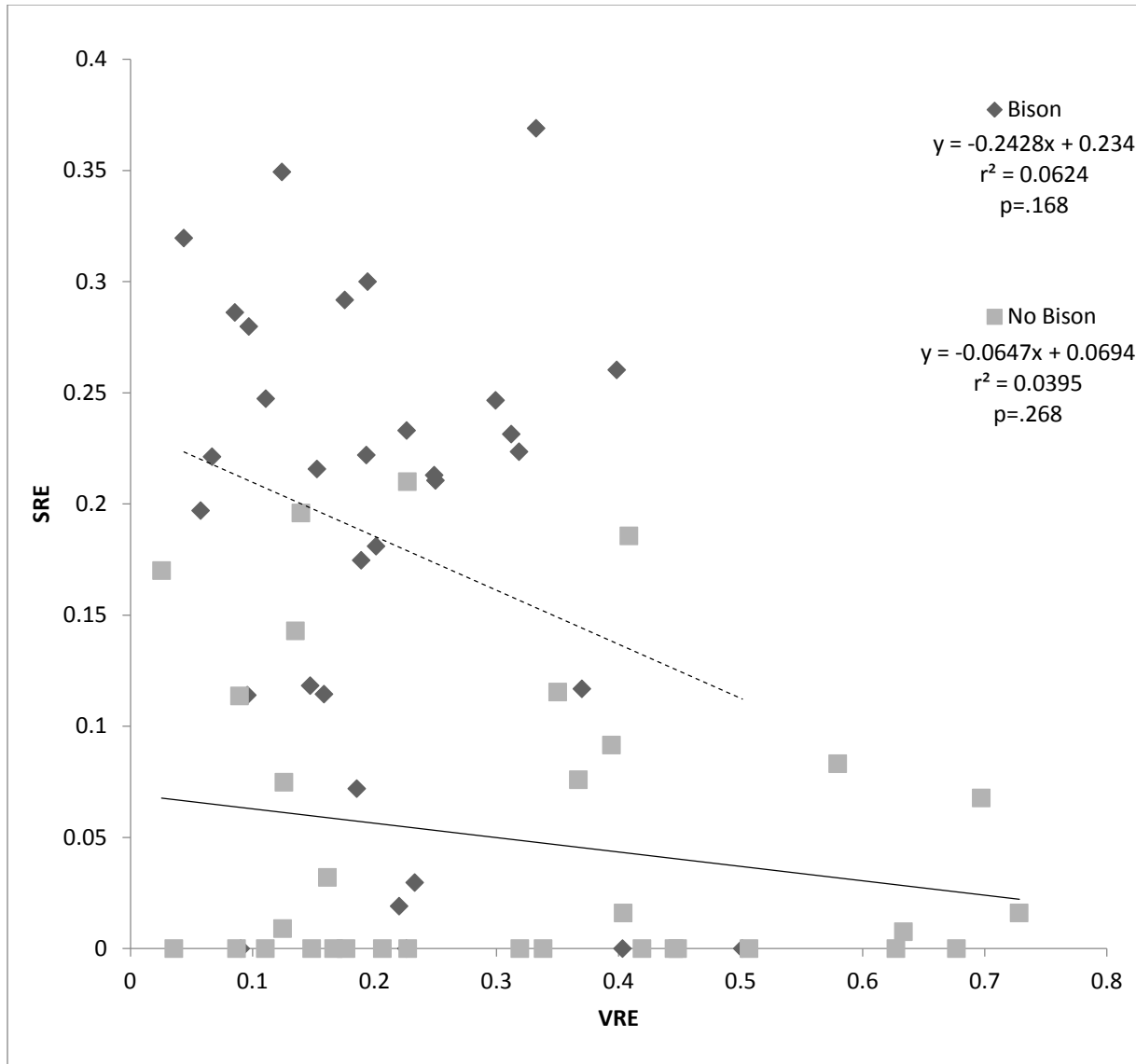
Figure 2.25 *Vernonia baldwinii*: Relationship between SRE and aboveground biomass (g) for individuals grown in habitats with and without bison.

Sexual Reproductive Effort (SRE) was calculated as the ratio of the total mass (g) of sexual reproductive structures to the total mass (g) of aboveground stems and leaves produced by each individual. The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA $r^2 = .655$, $p < .001$; main effects: Size $p = .012$, Grazing $p = .869$, Size*Grazing $p = .015$.
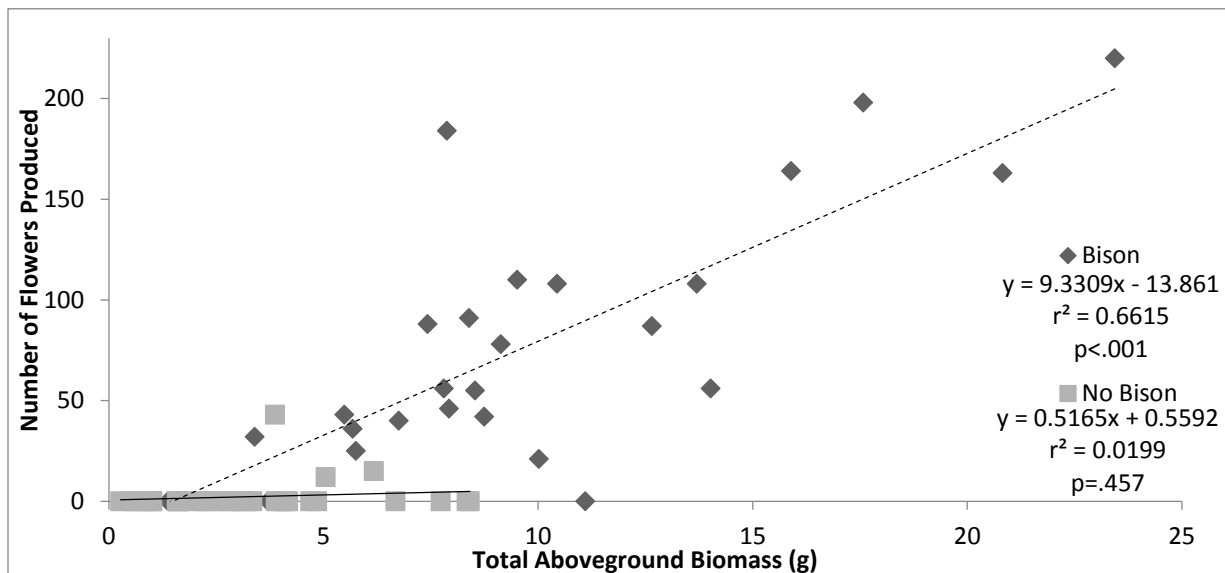

Figure 2.26 *Vernonia baldwinii*: Relationship between total masses (g) of sexual reproductive organs and aboveground vegetative parts for individuals grown in habitats with and without bison.

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA $r^2 = .650$, $p < .001$; main effects: Size $p < .001$, Grazing $p = .093$, Size*Grazing $p < .001$.

Figure 2.27 *Vernonia baldwinii***: Relationship between number of rhizomes produced and total aboveground biomass (g) for individuals grown in habitats with and without bison.**

The dashed trendline refers to individuals grown in habitats where bison were present.
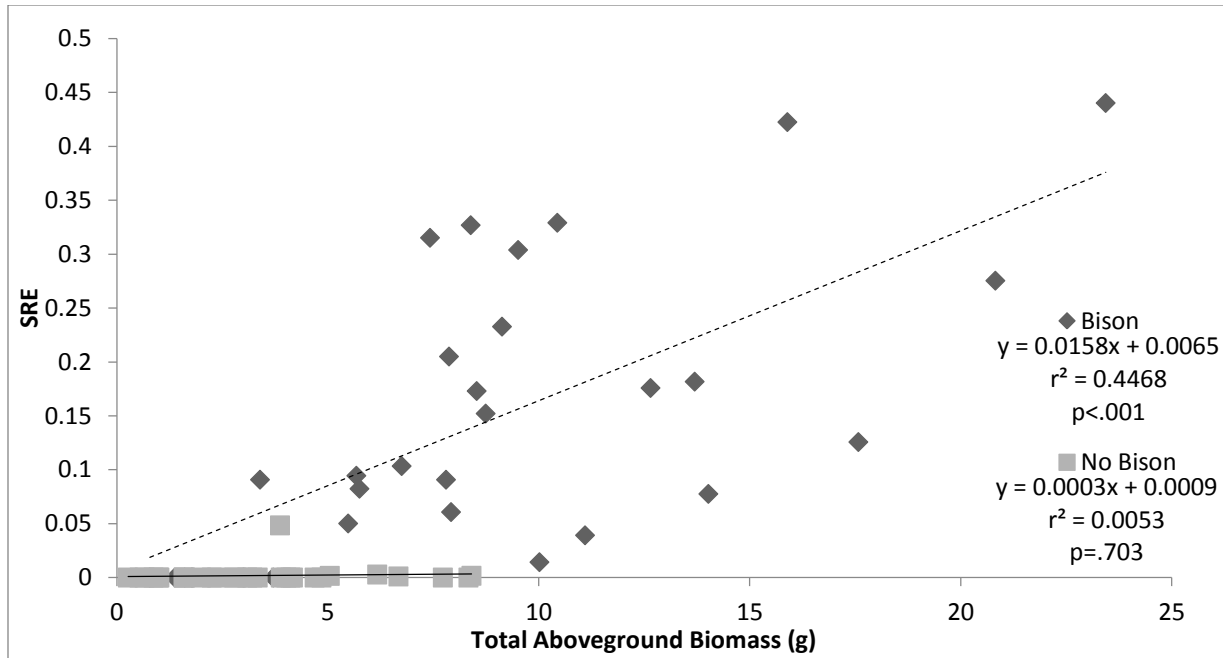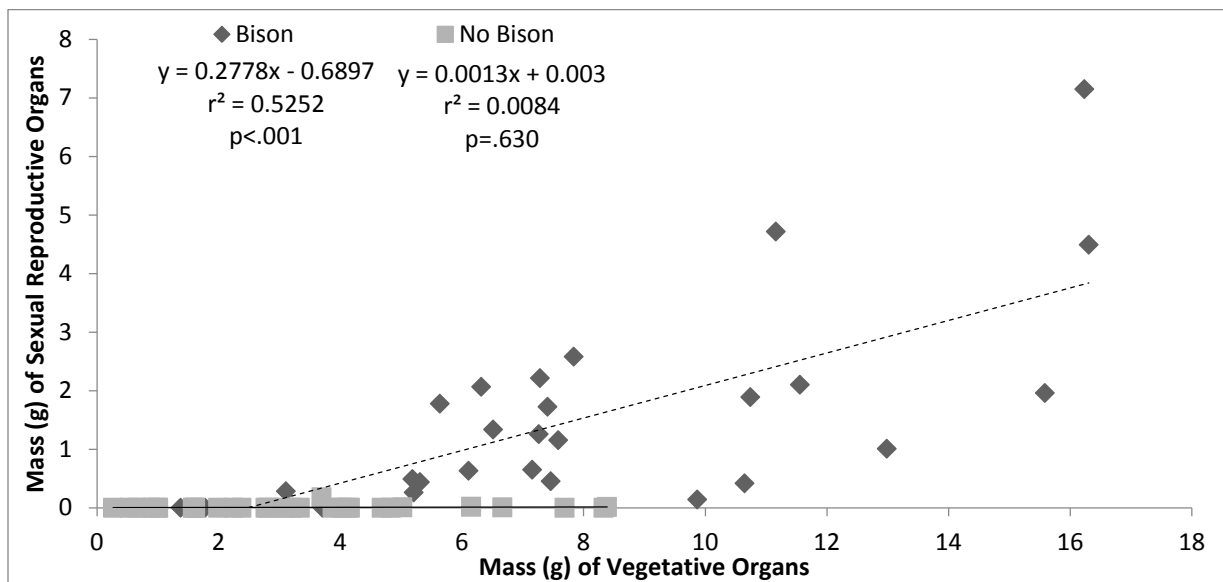ANCOVA r^2=.348, p<.001; main effects: Size p=.022, Grazing p=.129, Size*Grazing p=.810.

Figure 2.28 *Vernonia baldwinii***: Relationship between VRE and aboveground biomass (g) for individuals grown in habitats with and without bison.**

Vegetative Reproductive Effort (VRE) was calculated as the ratio of the total mass (g) of rhizomes to the total mass (g) of aboveground stems and leaves produced by each individual. The dashed trendline refers to individuals grown in habitats where bison were present.
ANCOVA r^2=.162, p=.019; main effects: Size p=.033, Grazing p=.591, Size*Grazing p=.617.
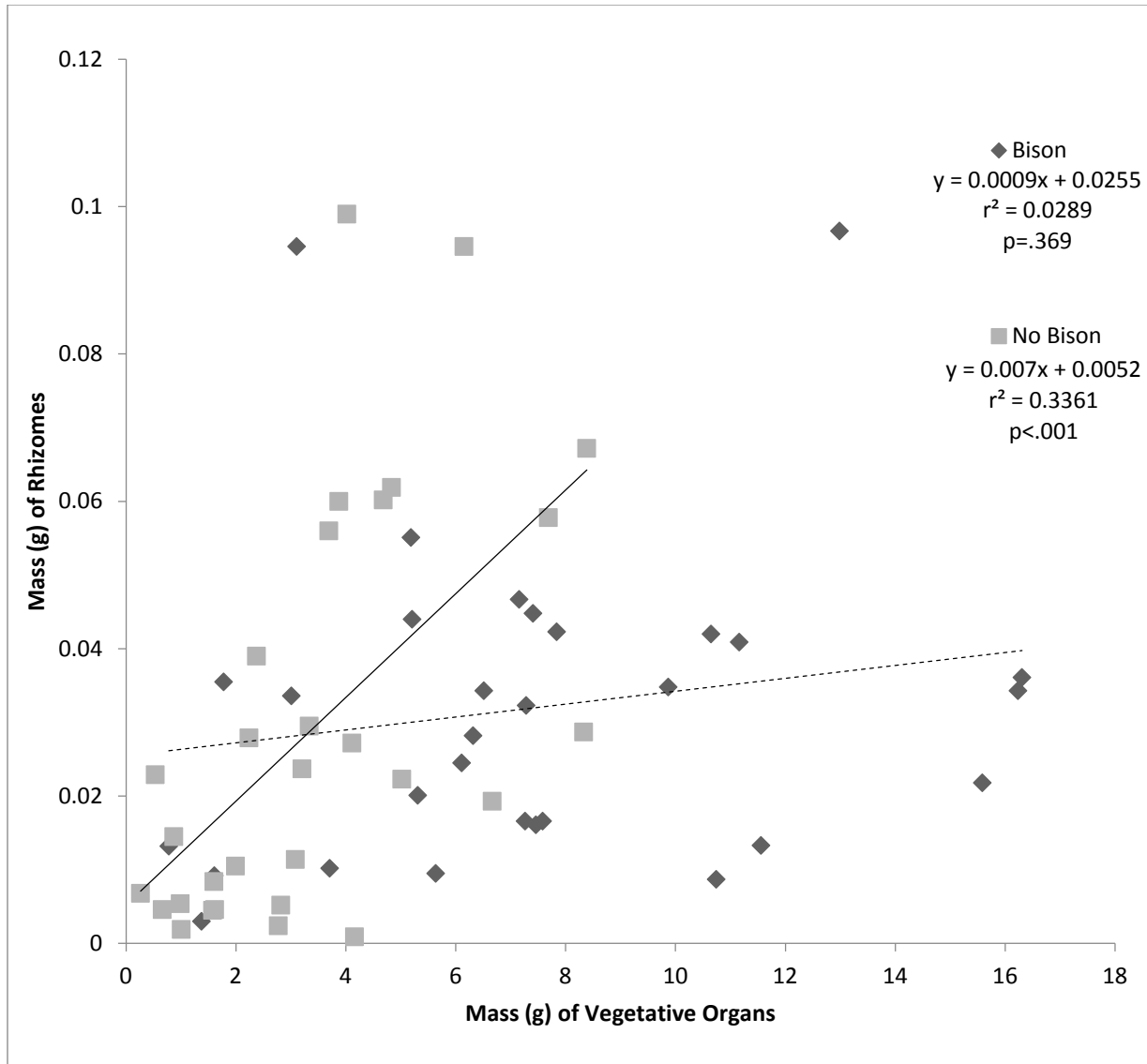
Figure 2.29 *Vernonia baldwinii*: **Relationship between total masses (g) of rhizomes and aboveground vegetative parts for individuals grown in habitats with and without bison.**

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.220, p=.003; main effects: Size p<.001, Grazing p=.077, Size*Grazing p=.004.

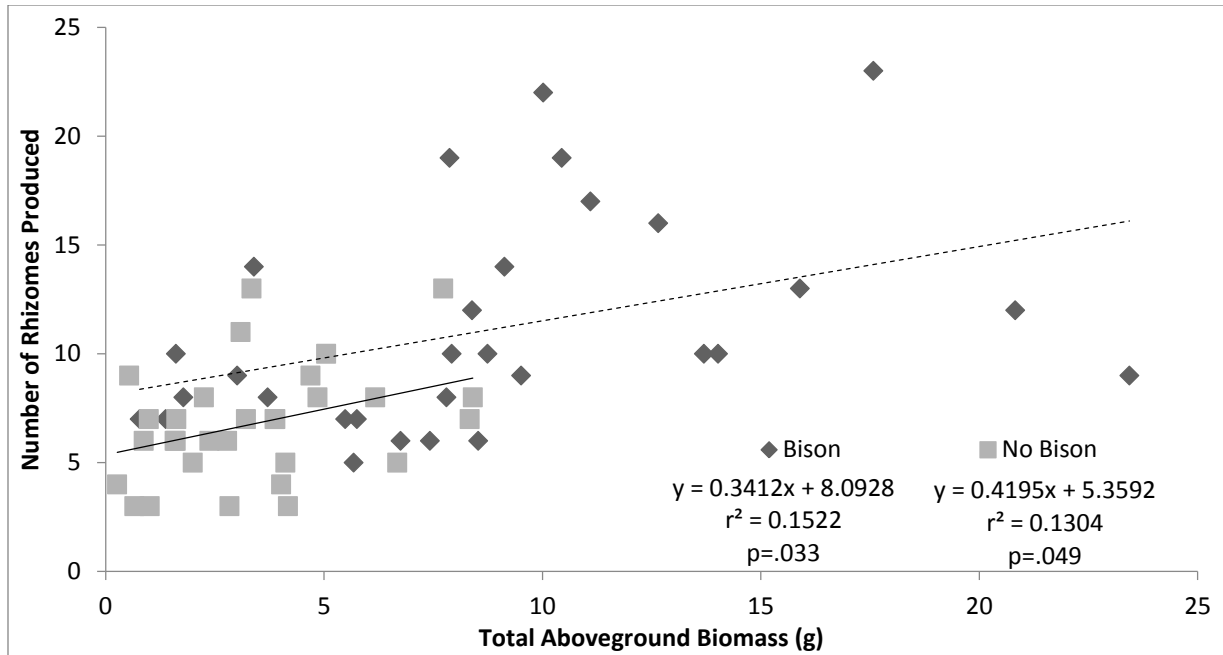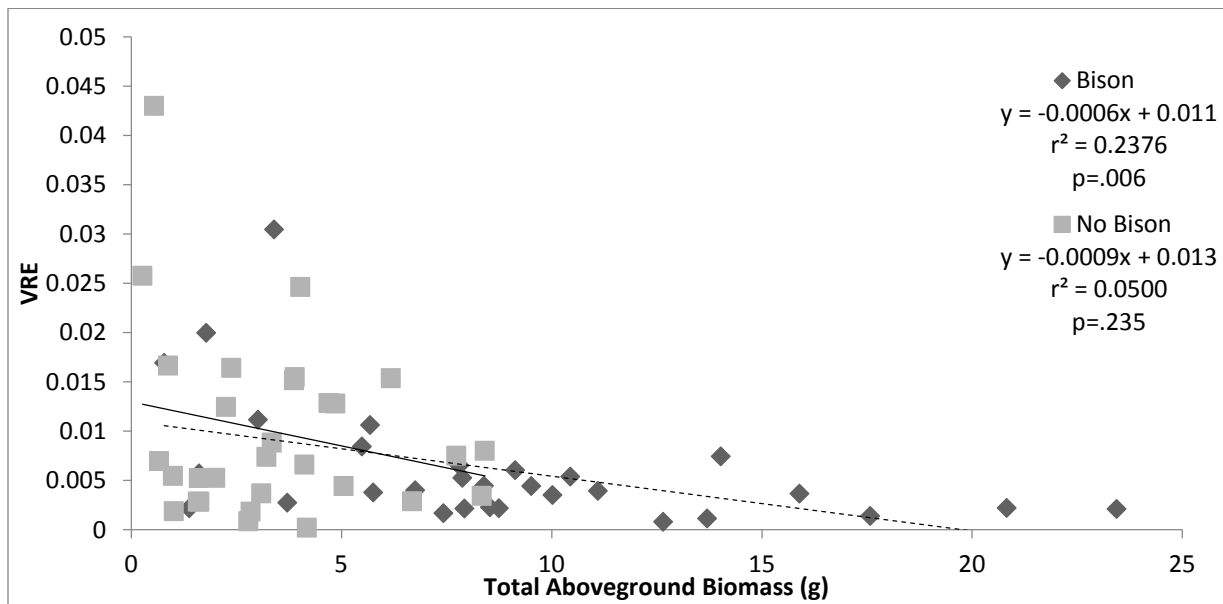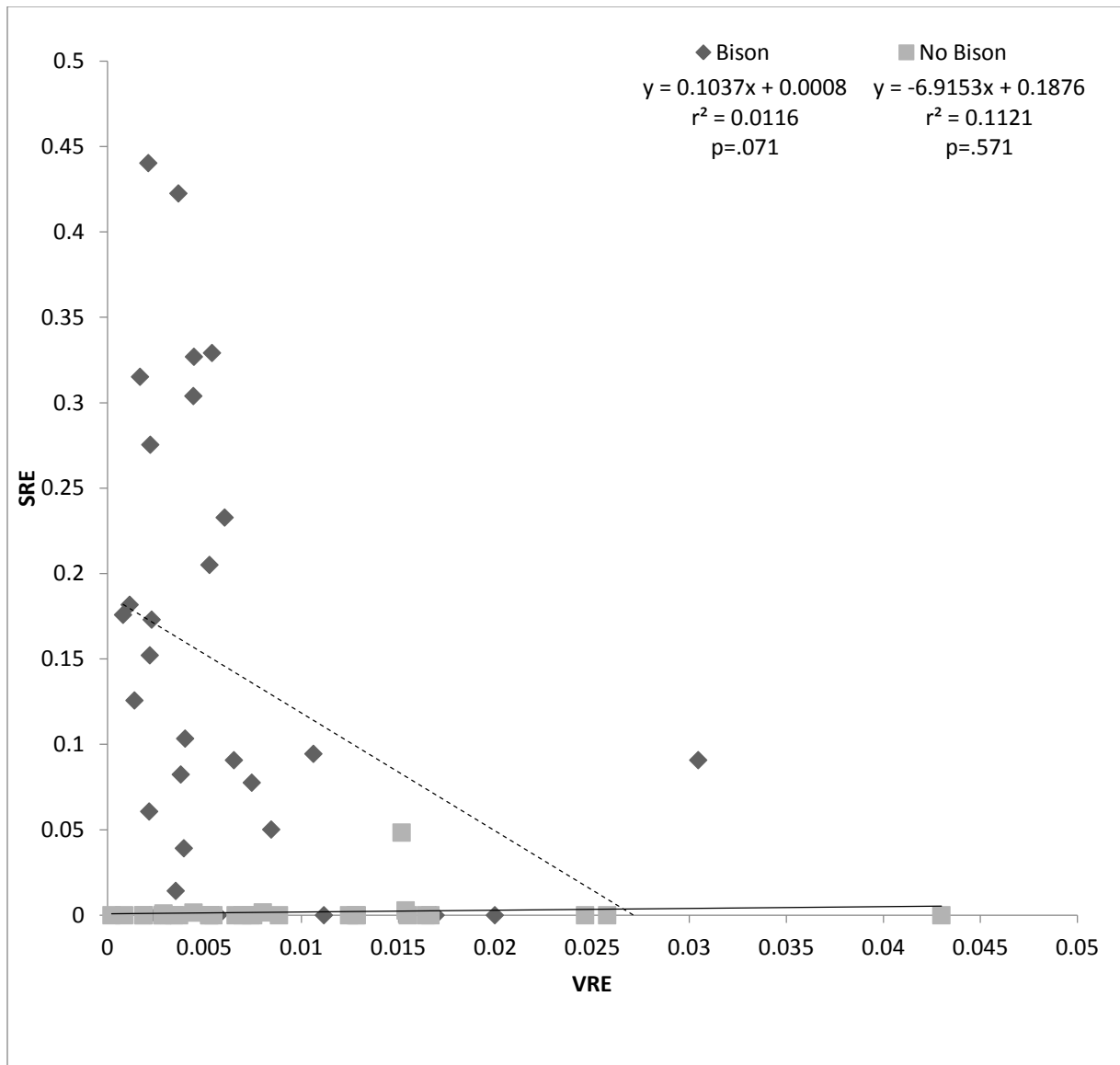**Figure 2.30** *Vernonia baldwinii*: **Relationship between SRE and VRE for individuals grown in habitats with and without bison.**

Sexual Reproductive Effort (SRE) was calculated as the ratio of the total mass (g) of sexual reproductive structures to the total mass (g) of aboveground stems and leaves produced by each individual. Vegetative Reproductive Effort (VRE) was calculated as the ratio of the total mass (g) of rhizomes to the total mass (g) of aboveground stems and leaves produced by each individual. The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.448, p<.001; main effects: VRE p=.037, Grazing p<.001, VRE*Grazing p=.032. ANCOVA r^2=.099, p=.118; main effects: SRE p=.567, Grazing p=.635, SRE*Grazing p=.444.

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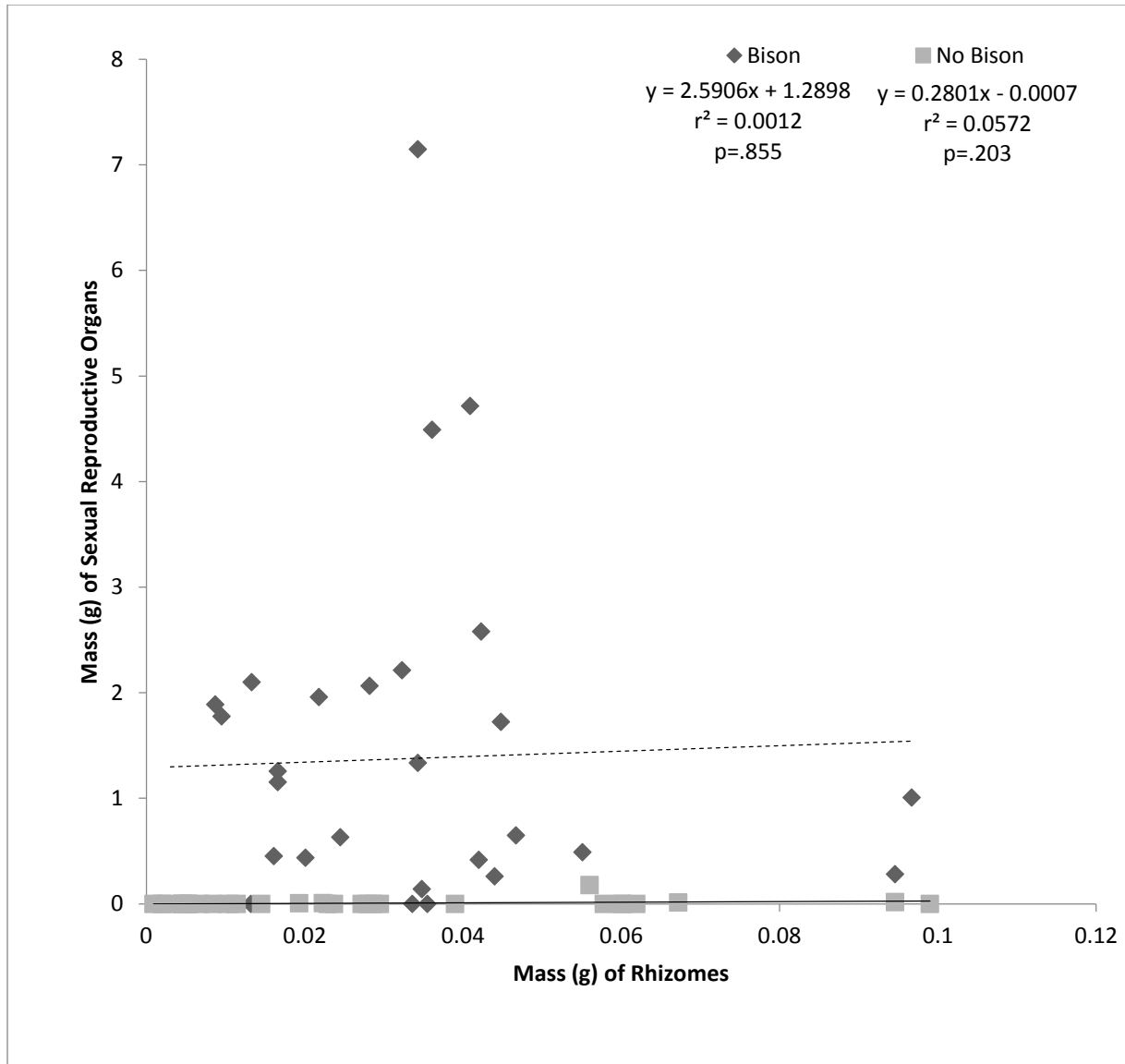
Figure 2.31 *Vernonia baldwinii***: Relationship between total masses (g) of sexual reproductive organs and rhizomes for individuals grown in habitats with and without bison.**

The dashed trendline refers to individuals grown in habitats with bison present. ANCOVA r^2=.264, p<.001; main effects: Rhizome Mass p=.822, Grazing p=.012, Rhizome Mass*Grazing p=.856. ANCOVA r^2=.038, p=.523; main effects: Floral Mass p=.158, Grazing p=.642, Floral Mass*Grazing p=.160.

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References

Augustine, D., and S. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. Journal of Wildlife Management 62:1165-1183.

Bark, D. 1987. Konza Prairie Research Natural Area, Kansas. Pages 45-46-50 In Greenland, D., editor. The climates of the long-term ecological research sites. Occasional paper no. 44, Insititute for Arctic and Alpine Research, University of Colorado, Boulder.

Bazzaz, F., N. Chiariello, P. Coley, and L. Pitelka. 1987. Allocating Resources to Reproduction and Defense. Bioscience 37:58-67.

Benot, M., C. Mony, J. Leps, L. Penet, A. Bonis, and J. Lepš. 2013. Are clonal traits and their response to defoliation good predictors of grazing resistance? Botany 91:62-68.

Benson, E., D. Hartnett, and K. Mann. 2004. Belowground bud banks and meristem limitation in tallgrass prairie plant populations. American Journal of Botany 91:416-421.

Blue, J., L. Souza, J. Schweitzer, N. Sanders, and A. Classen. 2011. The variable effects of soil nitrogen availability and insect herbivory on aboveground and belowground plant biomass in an old-field ecosystem. Oecologia 167:771-780.

Chabot, B. 1978. Environmental influences on photosynthesis and growth in Fragaria vesca. New Phytologist 80:87-98.

Chapin, D., L. Bliss, and L. Bledsoe. 1991. Environmental-regulation of nitrogen-fixation in a high arctic lowland ecosystem . Canadian Journal of Botany 69:2744-2755.

Charpentier, A., P. Grillas, and J. Thompson. 2000. The Effects of Population Size Limitation on Fecundity in Mosaic Populations of the Clonal Macrophyte Scirpus maritimus (Cyperaceae). American Journal of Botany 87:502-507.

Cheplick, G. 2005. The Allometry of Reproductive Allocation. Pages 97-98-128 In Reekie, E., and F. Bazzaz, editors. Reproductive Allocation in Plants, Elsevier Inc., Burlington.

Collins, S., A. Knapp, J. Briggs, J. Blair, and E. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280:745-747.

Coughenour, M. B. 1985. Graminoid Responses to Grazing by Large Herbivores: Adaptations, Exaptations, and Interacting Processes. Annals of the Missouri Botanical Garden 72:852-863.

Damhoureyeh, S., and D. Hartnett. 1997. Effects of bison and cattle on growth, reproduction, and abundances of five tallgrass prairie forbs. American Journal of Botany 84:1719-1728.

De Kroon, H., E. J. W. Visser, H. Huber, L. Mommer, and M. J. Hutchings. 2009. A modular concept of plant foraging behaviour: the interplay between local responses and systemic control. Plant Cell and Environment 32:704-712.

Dudley, S., and J. Schmitt. 1996. Testing the Adaptive Plasticity Hypothesis: Density-Dependent Selection on Manipulated Stem Length in Impatiens capensis. American Naturalist, The 147:445-465.

Eby, S., D. Burkepile, R. W. S. Fynn, C. Burns, N. Govender, N. Hagenah, S. Koerner, D. Thompson, K. Wilcox, S. Collins, K. Kirkman, A. Knapp, M. Smith, and K. J. Matchett. 2014. Loss of a large grazer impacts savanna grassland plant communities similarly in North America and South Africa. Oecologia 175:293-303.

England, R., and A. Devos. 1969. Influence of Animals on Pristine Conditions on the Canadian Grasslands. Journal of Range Management 22:87-94.

Evans, E. 1990. Dynamics of an Aggregation of Blister Beetles (Coleoptera, Meloidae) Attacking a Prairie Legume. Journal of the Kansas Entomological Society 63:616-625.

Fahnestock, J., and A. Knapp. 1994. Plant-responses to selective grazing by bison - interactions between light, herbivory and water-stress. Vegetatio 115:123-131.

Fay, P., J. Carlisle, A. Knapp, J. Blair, and S. Collins. 2003. Productivity responses to altered rainfall patterns in a C-4-dominated grassland. Oecologia 137:245-251.

Frank, D., and P. Groffman. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of yellowstone national park. Ecology 79:2229-2241.

Hajny, K. M., D. C. Hartnett, and G. W. T. Wilson. 2011. Rhus glabra response to season and intensity of fire in tallgrass prairie. International Journal of Wildland Fire 20:709-720.

Harper, J. L. 1977. Population Biology of Plants. Academic Press Inc., New York.

Hartemink, N., E. Jongejans, and H. De Kroon. 2004. Flexible life history responses to flower and rosette bud removal in three perennial herbs. Oikos 105:159-167.

Hartnett, D. C., K. R. Hickman, and L. E. F. Walter. 1996. Effects of Bison Grazing, Fire, and Topography on Floristic Diversity in Tallgrass Prairie. Journal of Range Management 49:413-420.

Hartnett, D. 1990. Size-dependent allocation to sexual and vegetative reproduction in 4 clonal composites. Oecologia 84:254-259.

Hautier, Y., C. Randin, J. Stoecklin, A. Guisan, and J. Stocklin. 2009. Changes in reproductive investment with altitude in an alpine plant. Journal of plant ecology 2:125-134.

Hermans, C., J. Hammond, P. White, and N. Verbruggen. 2006. How do plants respond to nutrient shortage by biomass allocation? Trends in plant science 11:610-617.

Hickman, K., D. Hartnett, R. Cochran, and C. Owensby. 2004. Grazing management effects on plant species diversity in tallgrass prairie. Journal of Range Management 57:58-65.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Range Management 60:695-713.

Holler, L., and W. Abrahamson. 1977. Seed and Vegetative Reproduction in Relation to Density in Fragaria virginiana (Rosaceae). American Journal of Botany 64:1003-1007.

Joern, A. 2005. Disturbance by fire frequency and bison grazing modulate grasshopper assemblages in tallgrass prairie. Ecology 86:861-873.

Johnson, L., and J. Matchett. 2001. Fire and grazing regulate belowground processes in tallgrass prairie. Ecology 82:3377-3389.

Karki, J., Y. Jhala, and P. Khanna. 2000. Grazing Lawns in Terai Grasslands, Royal Bardia National Park, Nepal1. Biotropica 32:423-429.

Karl, M. G., and R. A. Nicholson. 1987. Evaluation of the forage-disk method in mixed-grass rangelands of Kansas. Journal of Range Management 40:467-471.

Karlsson, P. S., and M. Mendez. 2005. The Resource Economy of Plant Reproduction. Pages 1-2-49 In Reekie, E., and F. Bazzaz, editors. Reproductive Allocation in Plants, Elsevier, Burlington.

Klimesova, J., and L. Klimes. 2007. Bud banks and their role in vegetative regeneration - A literature review and proposal for simple classification and assessment. Perspectives in Plant Ecology Evolution and Systematics 8:115-129.

Knapp, A. K., and T. R. Seastedt. 1986. Detritus Accumulation Limits Productivity of Tallgrass Prairie. Bioscience 36:662-668.

Knapp, A. K., D. C. Hartnett, and S. L. Collins. 1998. Grassland Dynamics: Long-term Ecological Research in Tallgrass Prairie. Oxford University Press, London.

Knapp, A. K., D. L. Hoover, J. M. Blair, G. Buis, D. E. Burkepile, A. Chamberlain, S. L. Collins, R. W. S. Fynn, K. P. Kirkman, M. D. Smith, D. Blake, N. Govender, P. O'Neal, T. Schreck, and A. Zinn. 2012. A test of two mechanisms proposed to optimize grassland aboveground primary productivity in response to grazing. Journal of Plant Ecology 5:357-365.

Knapp, A., J. Blair, J. Briggs, S. Collins, D. Hartnett, L. Johnson, and E. Towne. 1999. The keystone role of bison in north American tallgrass prairie - Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. Bioscience 49:39-50.

Koerner, S., and S. Collins. 2013. Small-scale patch structure in North American and South African grasslands responds differently to fire and grazing. Landscape Ecology 28:1293-1306.

La Pierre, K. J., S. Yuan, C. C. Chang, M. L. Avolio, L. M. Hallett, T. Schreck, and M. D. Smith. 2011. Explaining temporal variation in above-ground productivity in a mesic grassland: the role of climate and flowering. Journal of Ecology 99:1250-1262.

Liu, F., J. Chen, and Q. Wang. 2009. Trade-offs between sexual and asexual reproduction in a monoecious species Sagittaria pygmaea (Alismataceae): the effect of different nutrient levels. Plant Systematics and Evolution 277:61-65.

Lockhart, J. 1964. Physiological studies on light sensitive stem growth. Planta 62:97-115.

McCarthy, M. C., and B. J. Enquist. 2007. Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. Functional Ecology 21:713-720.

Mendoza, A., and M. Franco. 1998. Sexual Reproduction and Clonal Growth in Reinhardtia gracilis (Palmae), an Understory Tropical Palm. American Journal of Botany 85:521-527.

Moran, M. 2014. Bison Grazing Increases Arthropod Abundance and Diversity in a Tallgrass Prairie. Environmental Entomology 43:1174-1184.

N'Guessan, M., and D. C. Hartnett. 2011. Differential responses to defoliation frequency in little bluestem (Schizachyrium scoparium) in tallgrass prairie: implications for herbivory tolerance and avoidance. Plant Ecology 212:1275-1285.

Novakova, Z., J. Klimesova, T. Herben, Z. Nováková, J. Klimešová, L. Hrouda, and M. Rees. 2012. Species traits and plant performance: functional trade-offs in a large set of species in a botanical garden. Journal of Ecology 100:1522-1533.

Noy-Meir, I. 1993. Compensating Growth of Grazed Plants and Its Relevance to the Use of Rangelands. Ecological Applications 3:32-34.

Pastore, A., and F. L. Russell. 2012. Insect herbivore effects on resource allocation to shoots and roots in Lespedeza capitata. Plant Ecology 213:843-851.

Poorter, H., K. J. Niklas, P. B. Reich, J. Oleksyn, P. Poot, and L. Mommer. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytologist 193:30-50.

Powell, A. F. L. A. 2006. Effects of prescribed burns and bison (Bos bison) grazing on breeding bird abundances in tallgrass prairie. Auk, The 123:183-197.

Ronsheim, M. L., and J. D. Bever. 2000. Genetic Variation and Evolutionary Trade-Offs for Sexual and Asexual Reproductive Modes in Allium vineale (Liliaceae). American Journal of Botany 87:1769-1777.

Schmid, B., F. A. Bazzaz, and J. Weiner. 1995. Size Dependency of Sexual Reproduction and of Clonal Growth in 2 Perennial Plants. Canadian Journal of Botany-Revue Canadienne De Botanique 73:1831-1837.

Schulze, J., R. Rufener, A. Erhardt, and P. Stoll. 2012. The relative importance of sexual and clonal reproduction for population growth in the perennial herb Fragaria vesca. Population Ecology 54:369-380.

Sharrow, S. H. A Simple disk meter for measurement of pasture height and forage bulk. 1984. Journal of Range Management 37:94-95.

Shefferson, R., T. Kull, and K. Tali. 2006. Demographic response to shading and defoliation in two woodland orchids. Folia geobotanica 41:95-106.

Steinauer, E. M., and S. L. Collins. 1995. Effects of Urine Deposition on Small-Scale Patch Structure in Prairie Vegetation. Ecology 76:1195-1205.

Stuefer, J., and H. Huber. 1998. Differential effects of light quantity and spectral light quality on growth, morphology and development of two stoloniferous Potentilla species. Oecologia 117:1-8.

Sutherland, S., R. K. Sutherland, and Vickery. 1988. Trade-offs between sexual and asexual reproduction in the genus Mimulus. Oecologia 76:330-335.

Thompson, F. L., and C. G. Eckert. 2004. Trade-offs between sexual and clonal reproduction in an aquatic plant: experimental manipulations vs. phenotypic correlations. Journal of Evolutionary Biology 17:581-592.

Towne, E. 2002. Vascular plants of Konza Prairie biological station an annotated checklist of species in a Kansas tallgrass prairie. Sida, Contrib.Bot 20:269-294.

Underwood, N., and S. Halpern. 2012. Insect herbivores, density dependence, and the performance of the perennial herb Solanum carolinense. Ecology 93:1026-1035.

Veen, G. F. (., S. de Vries, E. Bakker, E. S. Bakker, and H. Olff. 2014. Grazing-induced changes in plant-soil feedback alter plant biomass allocation. Oikos 123:800-806.

Weiner, J., L. Campbell, J. Pino, and L. Echarte. 2009. The allometry of reproduction within plant populations. Journal of Ecology 97:1220-1233.

Wilson, G., A. Eom, and D. Hartnett. 2001. Effects of Ungulate Grazers on Arbuscular Mycorrhizal Symbiosis and Fungal Community Structure in Tallgrass Prairie. Mycologia 93:233-242.

Worley, A. C., and L. D. Harder. 1996. Size-Dependent Resource Allocation and Costs of Reproduction in Pinguicula Vulgaris (Lentibulariaceae). Journal of Ecology 84:195-206.

Xie, T., G. Zhang, Z. Zhao, G. Du, and G. He. 2014. Intraspecific competition and light effect on reproduction of Ligularia virgaurea, an invasive native alpine grassland clonal herb. Ecology and Evolution 4:827-835.